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PHYLOGENETIC IMPLICATIONS OF LEAF ANATOMY IN
SUBTRIBE MELITTIDINAE (LABIATAE) AND
RELATED TAXA

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Leaf anatomy was surveyed in 39 species of Labiatae, including representatives of all six genera of subtribe Melittidinae. When subjected to cladistic analysis, variation in stomatal subsidiary-cell configuration, glandular-trichome morphology, and leaf histology provides evidence for phylogenetic relationships among these genera. Peculiar saclike idioblasts in the mesophyll of *Physostegia* and *Brazoria* appear to represent a synapomorphy. This clade is further corroborated by the shared absence of bundle-sheath extensions, probably a derived state. Support for a more inclusive clade comprising *Physostegia*, *Brazoria*, and *Macbridea* is provided by the shared presence of a particular type of trichome and absence of keels on the secondary veins. Two other apparently derived states, diallelocytic stomata with four subsidiary cells and sessile glandular trichomes with partial radial walls, suggest that the sister group of the *Macbridea-Physostegia-Brazoria* clade is *Galeobdolon* or *Synandra*. Leaf anatomy provides no evidence that subtribe Melittidinae is monophyletic.

There is relatively little published information on the anatomy of the Labiatae, a rather surprising situation given the size and economic importance of the family. We are aware of only a few works on leaf anatomy in particular. The broadest in taxonomic scope are Solereder's (1908) general anatomical survey and Inamdar and Bhatt's (1972) study of stomatal types in the family. Other works, more intensive but narrower in taxonomic scope, are those of Bokhari and Hedge (1971) on tribe Meriandreae, Rudall (1979, 1980) on subtribe Hyptidinae, Azizian and Cutler (1982) on *Phlomis* L. and *Eremostachys* Ledeb., and Shah and Naidu (1983) on "tribe Ocimoideae."

The primary focus of this paper is the leaf anatomy of subtribe Melittidinae, but the study collection was selected to include a variety of other Labiatae so

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that it would be possible to evaluate the systematic significance of characters that vary within the Melittidinae. The work was undertaken with two objectives: first, to seek anatomical evidence for the monophyly (*sensu* Hennig, 1966) of subtribe Melittidinae and/or its suprageneric subgroups; and second, to contribute to the body of information available on the leaf anatomy of the Labiatae.

TAXONOMIC BACKGROUND

LABIATAE

The most widely used classification of the Labiatae today is that of Briquet (1895–1897), which is heavily based on a series of comprehensive treatments of the family by Bentham (1832–1836, 1848, 1876). Briquet's classification differs from Bentham's mainly in the ranking and interrelationships of suprageneric groups rather than in the content of those groups (Cantino & Sanders, 1986). The suprageneric groups of both authors are based principally on gross floral morphology.

An alternative classification of the Labiatae was proposed by Erdtman (1945) on the basis of palynological features. He subdivided the family into two subfamilies: Lamioideae, with tricolpate pollen that is shed in a two-celled stage; and Nepetoideae, with hexacolpate pollen shed in a three-celled stage. A variety of other characters have since been found to correlate with these (Wunderlich, 1967; Zoz & Litvinenko, 1979; Cantino & Sanders, 1986). Subfamily Lamioideae is characterized by albuminous seeds containing a spatulate embryo, the production of iridoid glycosides, the absence of rosmarinic acid, a low volatile terpenoid content (the leaves hence usually not aromatic), moderately unsaturated seed oils, and a nonmucilaginous pericarp. Subfamily Nepetoideae is characterized by exalbuminous seeds containing an "investing" embryo (terminology of Martin, 1946), the absence of iridoid glycosides, the production of rosmarinic acid, high volatile terpenoid content (the leaves hence aromatic), highly unsaturated seed oils, and a frequently mucilaginous pericarp. Erdtman's subfamilial classification (1945), with its strong character support, conflicts markedly with Briquet's (1895–1897) widely used system but is highly congruent with Bentham's (1876) tribal classification (Cantino & Sanders, 1986). In the present study, Erdtman's subfamilial classification has been adopted.

TRIBE LAMIEAE

Inasmuch as a primary objective of this study is to investigate whether subtribe Melittidinae is monophyletic, it is necessary to delimit a monophyletic study group that includes (but is not limited to) the subtribe. The Melittidinae fall within Erdtman's subfamily Lamioideae. Although this subfamily is a primary phenetic subgroup of the Labiatae, it has not been possible to demonstrate its monophyly through the identification of synapomorphies (Cantino & Sanders, 1986). There is, however, a less inclusive group that includes subtribe Melittidinae and appears to be monophyletic. It is composed of Bentham's (1876) tribes Lamieae and Prasieae, excluding *Anisomeles* R. Br., *Scutellaria*

L., and probably *Salazaria* Torrey. This group is similar in circumscription to Wunderlich's (1967) subfamily Lamioideae ("Stachyoideae"; corrected nomenclature follows Sanders & Cantino, 1984), but if it is recognized at the tribal level it must be called Lamieae. Except where otherwise stated, all future use of the name Lamieae will refer to the group thus circumscribed.

The monophyly of tribe Lamieae is supported by one clear synapomorphy, one probable synapomorphy, and a third congruent character, the polarity of which cannot currently be assessed. Hagemann and co-workers (1967) found an allenic component, which they presumed to be laballenic acid, in the seed oils of all examined members of Bentham's Lamieae and Prasieae except *Anisomeles* and *Scutellaria*. The allenic component was not found in these two genera or in the other examined members of Erdtman's subfamily Lamioideae, and it was found in only four of 122 examined species of subfamily Nepetoideae. The polarity of this character can be assessed by outgroup analysis (Watrous & Wheeler, 1981; Maddison *et al.*, 1984), using suprageneric taxa of the Verbenaceae as outgroups. (It is generally believed that the Labiatae evolved from the Verbenaceae, which would make the latter at best paraphyletic, but it is unclear which members of the Verbenaceae are the closest relatives of the Labiatae. All members of the Verbenaceae must therefore be included among the outgroups in the assessment of character polarity within the Labiatae.) In an unpublished study, Robert Kleiman (pers. comm.) found the allenic component to be absent from the seed oils of all 24 species of Verbenaceae examined, including representatives of three subfamilies and eight tribes. Occurrence of the allenic component therefore appears to be a derived trait within the Labiatae and represents a synapomorphy of a monophyletic group composed of Bentham's tribes Lamieae and Prasieae (excluding *Scutellaria* and *Anisomeles*). Because *Salazaria* appears to be closely related to *Scutellaria* on morphological (Epling, 1942) and chemical (Kooiman, 1972) grounds, it should perhaps be excluded from the Lamieae as well, although its seed oils have not been investigated.

Embryological peculiarities of the Lamieae offer two other possible synapomorphies. The mature embryo sac in the Labiatae tends to be two-lobed, with distinct micropylar and chalazal sections. Genera differ in the relative size and shape of these lobes. Wunderlich (1967) reported that the micropylar lobe is much longer and broader than the chalazal one in Bentham's Lamieae and Prasieae (except *Scutellaria* and *Anisomeles*), whereas the micropylar lobe is shorter than or equal to the chalazal in the rest of the Labiatae, except two genera of Nepetoideae. *Salazaria* was not examined. Embryo-sac shape has been reported for ten genera of Verbenaceae representing three subfamilies and six tribes (Junell, 1934; Misra, 1939; Tatachar, 1940; Pal, 1951; Maheshwari, 1954; Khaleel & Nalini, 1972; Spies & Stirton, 1982; Spies, 1984a, 1984b; Thirumaran & Lakshmanan, 1984). In only one species, *Clerodendrum ugandense* Prain, does the embryo sac resemble those found in the Lamieae (Junell, 1934). In all other Verbenaceae examined, including four other species of *Clerodendrum* L. (Junell, 1934; Misra, 1939), the micropylar end of the embryo sac is usually little if at all broader (in some species narrower) than the chalazal end; if it is much broader, it is shorter than the chalazal end. The characteristic

embryo-sac shape of the Lamieae is thus probably derived, although more Verbenaceae need to be studied before character polarity can be assessed with confidence.

Wunderlich (1967) reported the presence of what Schnarf (1918) called "Lamium-type" glandular trichomes (identical to our "type 4"; see trichome classification below) on the outside of the integument in recently fertilized ovules of all examined genera of Bentham's Lamieae and Prasieae except *Scutellaria* and *Anisomeles*; no such glandular trichomes were found in other Labiatae (but *Salazaria* was not examined). It is not possible to assess the polarity of this character because of lack of data for the Verbenaceae, but its distribution in the Labiatae closely parallels that of the other two characters.

Although a strong case can be made for the existence of a monophyletic tribe Lamieae (as circumscribed above), one must remain aware that the characters delimiting the group have been examined in a minority of its members. Seed-oil chemistry was studied (Hagemann *et al.*, 1967) in 18 of the 42 genera of Bentham's (1876) Lamieae and Prasieae, and the two embryological characters cited above were studied in 16 genera of these tribes (Wunderlich, 1967). There are 11 genera for which data are available for all three characters. Because the congruence between the three characters is perfect in these genera, we are assuming that the characters are highly correlated in the group as a whole. Examination of more genera may demonstrate, however, that others besides *Scutellaria* and *Anisomeles* are not members of the monophyletic group. Our tentative inclusion of all of Bentham's Lamieae and Prasieae (except *Scutellaria*, *Anisomeles*, and possibly *Salazaria*) reflects our confidence in Bentham's usually excellent taxonomic judgment—i.e., we are assuming that those genera not yet examined for embryology and seed-oil chemistry really are closely related to those that have been.

SUBTRIBE MELITTIDINAE

The historical changes in the circumscription of subtribe Melittidinae have been summarized by Cantino (1985a). As currently circumscribed, the subtribe comprises six genera, four of them (*Brazoria* Engelm. ex A. Gray, *Macbridea* Elliott ex Nutt., *Physostegia* Bentham, and *Synandra* Nutt.) North American, one (*Chelonopsis* Miq.) Asian, and one (*Melittis* L.) European. The group is delimited on the basis of a set of calyx and corolla characters that were proposed by Bentham (1876) and adopted by Briquet (1895–1897): calyx broadly campanulate, membranaceous or herbaceous, 3- or 4-lobed or 5-toothed, with venation scarcely visible; corolla tube long-exserted from calyx, broad at base or markedly dilated distally, with upper lip broad and scarcely concave.

A survey of these characters in subfamily Lamioideae (Cantino, unpublished data) revealed that none is diagnostic of subtribe Melittidinae. Three states used by Bentham and Briquet (calyx broadly campanulate, calyx membranaceous or herbaceous, and corolla tube long-exserted from the calyx) are present throughout the Melittidinae but are also common elsewhere in the subfamily. The other character states cited by these authors are not only found elsewhere in the subfamily but also occur in only some members of the Melittidinae.

Weak calyx venation at anthesis is characteristic of *Physostegia*, *Brazoria*, and (to a degree) *Synandra*, but not the other three genera. The upper lip of the corolla is broad and only barely concave in *Physostegia*, *Chelonopsis*, and three species of *Brazoria* but markedly concave in *Macbridea*, *Synandra*, and *Brazoria scutellarioides*. The number of calyx lobes varies from three to five, with no two genera having the same calyx morphology. Corolla-tube shape is similarly variable. It is, of course, insufficient to consider characters only singly. In groups in which parallel and/or reticulate evolution have been common, taxa are often distinguished by combinations of character states, with no single state unique to any taxon ("kaleidoscopic variation"; see Cantino, 1982). However, the combination of the three character states that occur throughout the Melittidinae is also found in some or all species of at least ten other genera in subfamily Lamioideae (*Colquhounia* Wallich, *Gomphostemma* Benth, *Lamium* L., *Microtoena* Prain, *Phyllostegia* Benth, *Scutellaria*, *Stenogyne* Benth, *Tetraclea* A. Gray, *Thuspeinanta* T. Durand, and *Trichostema* L.), seven of them in tribe Lamieae as circumscribed above.

We are unaware of any morphological feature or combination of features that would distinguish subtribe Melittidinae from the rest of tribe Lamieae, let alone a clearly derived feature. Nor does cytology provide evidence for the monophyly of the subtribe. Chromosome number is extremely variable among the genera, chromosome size is moderately variable, and other karyotypic features are restricted to particular species or species groups (Cantino, 1985a). The present study was undertaken to investigate whether leaf anatomy might provide evidence for the monophyly of subtribe Melittidinae, where morphology and cytology have not.

STOMATAL TERMINOLOGY

Because of the variety of stomatal classifications now available and the sometimes conflicting use of terms contained therein, a brief review of the situation is necessary if the reader is to understand our adopted terminology. For a more comprehensive and very enlightening review, see Rasmussen (1981).

Stomata have been classified on the basis of three criteria: the configurations of neighboring and subsidiary cells in mature stomata (Vesque, 1889; Metcalfe & Chalk, 1950; Payne, 1970), stomatal ontogeny (Pant, 1965; Stevens & Martin, 1978; Payne, 1979), and a combination of the above (Fryns-Claessens & Van Cotthem, 1973; Stevens & Martin, 1978).

The first criterion is relatively uncomplicated and has the advantage that it can be applied when one is working with mature leaves. Its principal disadvantage is that the same stomatal morphology may develop through different ontogenetic pathways in different plants and may therefore not be homologous (Rasmussen, 1981, and references cited therein). Classifications based partly or completely on stomatal ontogeny are more difficult to apply, and some of the terms used are defined differently by different authors.

Pant (1965) classified stomata on the basis of their ontogenetic pathways: mesogenous stomata, in which the guard-cell mother cell and all subsidiaries are derived from the same meristemoid; perigenous stomata, in which all

neighboring and subsidiary cells are derived from protodermal cells other than the meristemoid that produces the guard-cell mother cell; and mesoperigenous stomata, in which the surrounding cells are of dual origin, some mesogenous and others perigenous.

The guard-cell mother cell is the immediate progenitor of the guard cells. Subsidiary cells surround the guard cells and clearly differ from other epidermal cells; neighboring cells immediately surround the guard cells but do not differ in shape from the remaining epidermal cells (Fryns-Claessens & Van Cotthem, 1973; Rasmussen, 1981). Unfortunately, the ambiguity of the term "meristemoid" has rendered Pant's and other ontogenetic classifications difficult to use.

Stomatal ontogeny starts with the unequal division of a protodermal cell. The smaller daughter cell, which contains a denser cytoplasm, divides again unequally or directly produces (by an equal division) the pair of guard cells (Fryns-Claessens & Van Cotthem, 1973; Payne, 1979; Rasmussen, 1981). The term "meristemoid" was used by Fryns-Claessens and Van Cotthem (1973) and Rasmussen (1981) to refer to the smaller daughter cell of the original protodermal cell, whereas Payne (1979) referred to the protodermal cell itself as the meristemoid. If the latter usage is adopted, there is always at least one neighboring or subsidiary cell that is derived from the meristemoid (i.e., mesogenous), so a true perigenous type cannot exist (Fryns-Claessens & Van Cotthem, 1973; Payne, 1979). A consequent disadvantage of Payne's terminology is that it is less precise; i.e., a wider variety of ontogenetic pathways is necessarily subsumed under the same term, mesoperigenous (see *fig. 3* in Rasmussen, 1981). For this reason, and because the meristemoid *sensu* Payne can only be recognized after it has divided and hence no longer exists (Rasmussen, 1981), the ontogenetic terminology of Fryns-Claessens and Van Cotthem (1973) rather than that of Payne (1979) is adopted in this study. The more complex system of Stevens and Martin (1978) is even more precise but is not used here because of the difficulty in distinguishing "agene" cells (Rasmussen, 1981) from perigene cells *sensu* Rasmussen.

MATERIALS AND METHODS

Leaf material was obtained from 53 specimens representing 39 species (see APPENDIX 1), including all species of *Brazoria*, *Macbridea*, *Melittis*, and *Synandra*, seven of the 12 species of *Physostegia*, and two of the approximately 16 species of *Chelonopsis*. Leaf material of most species was collected from living plants, with herbarium specimens prepared as vouchers. Leaf material of *Chelonopsis*, *Melittis*, and some species of *Physostegia* was obtained directly from herbarium specimens.

Fresh leaves were fixed in Carnoy's solution (3 parts ethanol to 1 part acetic acid). Dried leaves were revived by soaking them in 5 percent sodium hydroxide for three days at room temperature. Both types of material were then stored in 70 percent ethanol. To prepare the material for study, we used the whole-mount method as well as transverse sectioning of the lamina. In the former method leaves or leaf pieces were stained with ferric tannate (2.5% tannic acid

in 50% ethanol, followed by 2.5% ferric chloride in 50% ethanol; modified from Berlyn & Miksche, 1976) and mounted in surface view. In the latter, leaves were infiltrated with and embedded in paraffin (Cutler, 1978) and sectioned at 10- μ m thickness with an AO rotary microtome. After sectioning, the leaves were stained with toluidine blue or with safranin O and fast green FCF. The procedure using toluidine blue is outlined in Sakai (1973). The double-staining procedure, adapted from Johansen (1940), required deparaffination of the sections, staining with safranin (1% in 50% ethanol) and fast green (0.1% in 50% ethanol), dehydration through a series of ethanol, xylene:ethanol (1:1), and xylene, and mounting in Permount.

A set of permanent slides has been deposited in the Bartley Herbarium of Ohio University (BHO). Drawings were prepared by means of a microprojector or the camera-lucida attachment of an Olympus BH-2 microscope.

RESULTS

STOMATA

Based on shapes and arrangements of mature subsidiary and neighboring cells, the following types of stomata were found in the species examined (see FIGURE 1) (definitions follow Payne, 1970, 1979; and Wilkinson, 1979): anomocytic (stoma surrounded by a limited number of cells that are indistinguishable from other epidermal cells); paracytic (stoma bordered on both sides by one or more subsidiary cells whose long axes lie parallel with the long axis of the guard cells; subsidiary cells sometimes meeting over the poles and sometimes laterally elongated); anisocytic (stoma surrounded by three cells, one of which is markedly smaller than the other two); diacytic (stoma enclosed by a pair of subsidiary cells whose common radial walls are at right angles to the guard cells); and diallelocytic (stoma enclosed by three or more C-shaped cells at right angles to the guard cells).

Two subtypes of diallelocytic stomata were found in the species examined, one with three subsidiary cells and the other with four. The two have not been distinguished by previous authors, including Payne (1970), who discussed the ontogeny of diallelocytic stomata. Since the two types do not always occur together (see TABLES 1, 2), they are worth distinguishing. The three-celled type will be referred to as diallelocytic-1 and the four-celled type as diallelocytic-2.

The ontogenetic pathways of several stomatal types were documented through examination of young leaves in various stages of development (see FIGURE 1). The diallelocytic-1 type was studied in *Scutellaria lateriflora*, *Stachys riddellii*, and *Stachys tenuifolia* and is mesoperigenous in all. Because the diallelocytic-2 type occurs only with the diallelocytic-1 type in the species examined (although the latter may occur without the former), and the former differs from the latter in having one more subsidiary cell, the ontogenetic pathway reported by Payne (1970) for the diallelocytic-2 type is presumed to occur in the taxa examined in this study. The ontogenetic pathway for the diacytic type was also adopted from Payne (1970). The ontogeny of the anomocytic type was studied in *Scutellaria lateriflora*, *Stachys tenuifolia*, and *Stachys riddellii* and is perigenous

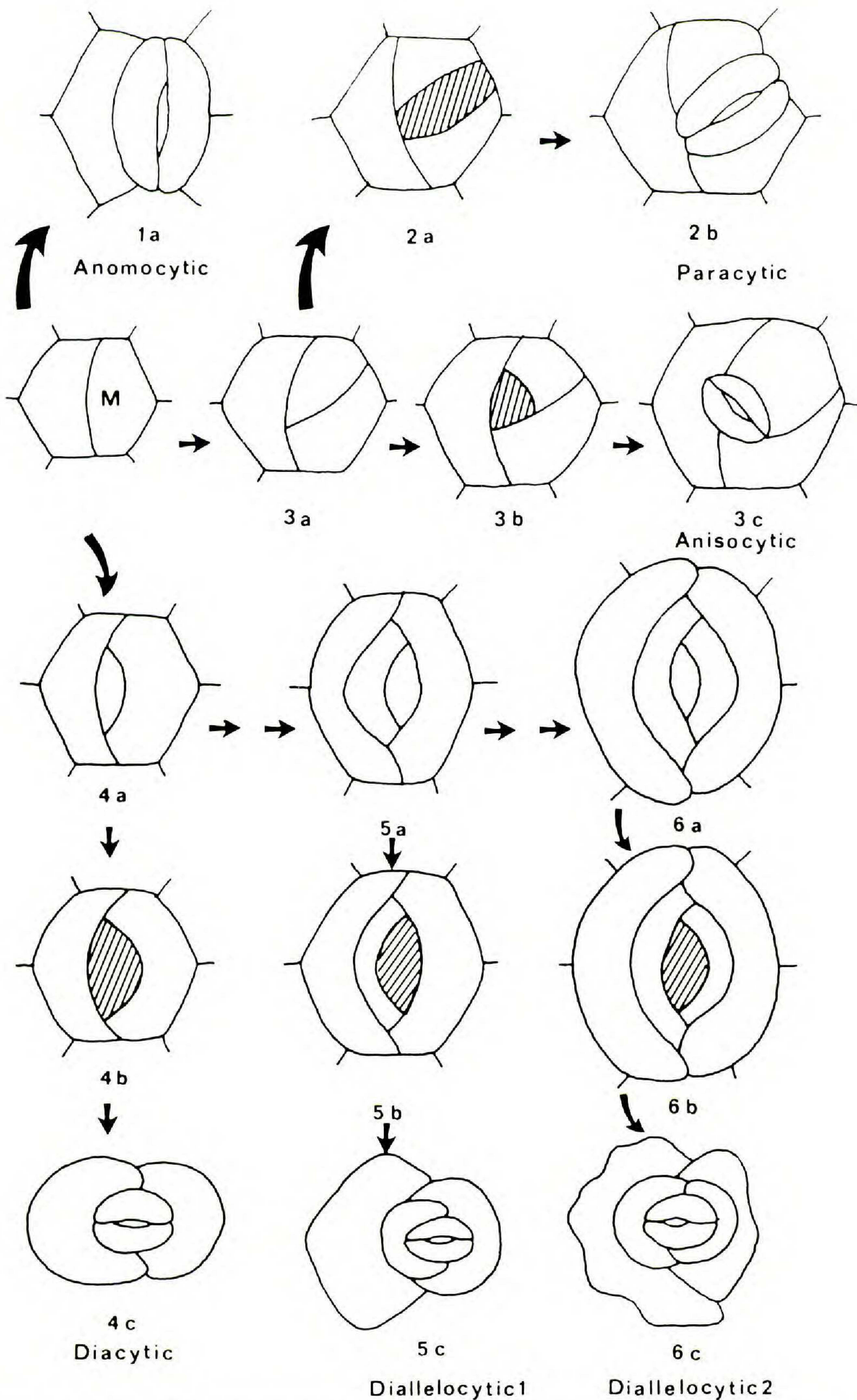


FIGURE 1. Stomatal ontogenetic pathways: anomocytic (1a), paracytic (2a, b), anisocytic (3a-c), diacytic (4a-c), diallelocytic-1 (5a-c), and diallelocytic-2 (6a-c). M = meristemoid (*sensu* Fryns-Claessens & Van Cotthem). Diacytic and diallelocytic-2 ontogenies adopted from Payne (1970).

in all. The ontogeny of the paracytic and anisocytic types was studied in *Trichostema dichotomum*. Both are mesoperigenous, and they share a common initial step in their ontogenetic pathways.

Other stomatal features examined included distribution (viz., both leaf surfaces or abaxial surface only), position in relation to general level of epidermis (viz., sunken or raised), and presence of stomatal ledges. Stomatal ledges are elevated extensions of the cuticle that rise from the guard-cell surface "like an incompletely roofed dome" (Wilkinson, 1979, p. 97). They extend over the stomatal pore, delimiting an outer cavity (see *fig. 10.1* in Wilkinson, 1979). In some taxa similar inner ledges project from the guard cells, forming an inner cavity (Wilkinson, 1979), but only outer ledges were found in the present study.

Published data on stomatal types in Labiatae and Verbenaceae are scarce, and the authors do not always clearly indicate the taxonomic distribution of stomatal types. Data from Inamdar (1969), Ramayya and Rao (1969), Payne (1970), and Inamdar and Bhatt (1972) are summarized in TABLE 1; our own observations are shown in TABLE 2.

Diacytic, diallelocytic-1, and anomocytic stomata are all common in the Labiatae. Of the 39 species we examined, diallelocytic-1 stomata were found in 31, diacytic in 33, and anomocytic in 24. Diacytic and anomocytic stomata occur widely in both the Labiatae and the Verbenaceae, but diallelocytic-1 stomata are apparently rare in the Verbenaceae, having been reported only from *Lippia lanceolata*.

Diallelocytic-2 stomata have been observed in seven genera of Labiatae and one of Verbenaceae. Specifically, we observed this type in six of seven examined species of *Physostegia*, both species of *Macbridea*, one of the four species of *Brazoria*, the single species of *Galeobdolon* Adanson, and two of the seven examined species of *Scutellaria*; it has also been reported from *Ocimum* L., *Plectranthus* L'Hér., and *Lippia* L.

Anisocytic stomata appear to be rare in the Labiatae. We found them only in *Trichostema* and *Prostanthera* Labill. In previous studies anisocytic stomata have been reported from three species of Verbenaceae but not in any Labiatae. We found paracytic stomata only in *Trichostema*, *Prostanthera*, and *Melittis*, and in the latter two they are rare; they have also been reported from three species of Verbenaceae. Parallelocytic stomata (Payne, 1970), which resemble the diallelocytic-2 type but have the subsidiary cells parallel to the guard cells, have been found in *Lippia lanceolata* (Abu-Asab, 1984) but not in any Labiatae. Helicocytic stomata (Payne, 1970) were included in the drawing of *Lavandula gibsonii* in Inamdar and Bhatt (1972, *fig. 13*).

Leaves are amphistomatic in the North American Melittidinae, *Scutellaria integrifolia*, and the examined species of *Ajuga* L., *Trichostema*, *Lamium*, *Marrubium* L., and *Prostanthera*. They are hypostomatic in the rest of the Labiatae examined, including *Chelonopsis* and *Melittis* of subtribe Melittidinae. Most species of Labiatae and Verbenaceae investigated in previous studies have hypostomatic leaves. We found intrageneric variation in this character in *Scutellaria*, and such variation has also been reported in *Leucas* R. Br. and *Ocimum* (Inamdar & Bhatt, 1972), *Eriope* Humb. & Bonpl. ex Benth (Rudall, 1979), and *Phlomis* (Azizian & Cutler, 1982).

TABLE 1. Published data on stomatal types in Labiatae and Verbenaceae.^a

Species	Stomatal Types ^b								St. Loc. ^c	Ref. ^d
	1	2	3	4	5	6	7	8		
Labiatae										
Subfamily Lamioideae										
Tribe Lamieae										
<i>Leonotis nepetifolia</i> R. Br.	+	-	-	+	-	-	-	-	H	3
<i>Leucas aspera</i> Sprengel	+	+	-	+	-	-	-	-	A	3
<i>L. biflora</i> R. Br.	+	-	-	+	-	-	-	-	H	3
<i>L. cephalotes</i> Sprengel	+	+	-	+	-	-	-	-	H	3
<i>L. linifolia</i> Sprengel	+	-	-	+	-	-	-	-	H	3
<i>L. urticifolia</i> R. Br.	+	-	-	+	-	-	-	-	H	3
<i>L. zeylanica</i> R. Br.	+	-	-	+	-	-	-	-	A	3
<i>Phlomis bracteosa</i> Royle ex Bentham	-	+	-	+	-	-	-	-	H	3
Other Lamioideae										
<i>Anisomeles heyneana</i> Bentham	+	-	-	+	-	-	-	-	H	3
<i>A. ovata</i> R. Br.	+	+	-	+	-	-	-	-	H	3
<i>Dysophylla auricularia</i> Blume	-	+	-	+	-	-	-	-	H	3
<i>Pogostemon parviflorus</i> Bentham	+	-	-	+	-	-	-	-	H	3
<i>P. purpurascens</i> Dalz.	+	+	-	+	-	-	-	-	H	3
Subfamily Nepetoideae										
Tribe Mentheae										
<i>Mentha viridis</i> L.	+	+	-	+	-	-	-	-	H	3
<i>Micromeria capitata</i> Bentham	+	-	-	+	-	-	-	-	H	3
Tribe Ocimeae										
<i>Acrocephalus capitatus</i> Bentham	+	+	-	+	-	-	-	-	H	3
<i>Coleus amboinicus</i> (Bentham) Lour.	+	-	-	+	-	-	-	-	H	3
<i>C. blumei</i> Bentham	+	+	-	+	-	-	-	-	H	3
<i>Hyptis suaveolens</i> (L.) Poit.	+	-	-	+	-	-	-	-	H	3
<i>Lavandula burmanii</i> Bentham	+	-	-	+	-	-	-	-	H	3
<i>L. gibsonii</i> J. Graham	+	-	-	+	-	-	+	-	H	3
<i>Moschosma polystachyum</i> Bentham	+	-	-	+	-	-	-	-	H	3
<i>Ocimum adscendens</i> Willd.	+	+	-	+	-	-	-	-	?	5
<i>O. basilicum</i> L.	+	+	-	+	-	-	-	-	A	3
<i>O. basilicum</i> L.	+	+	+	+	-	-	-	-		5
<i>O. canum</i> Sims	+	+	-	+	-	-	-	-	H	3
<i>O. gratissimum</i> L.	+	-	-	+	-	-	-	-	H	3
<i>O. kilimandscharicum</i> Gürke	+	-	-	+	-	-	-	-	H	3
<i>O. sanctum</i> L.	+	-	-	+	-	-	-	-	H	3
<i>O. sanctum</i> L.	+	-	-	+	-	-	-	-		5
<i>Orthosiphon pallidus</i> Royle ex Bentham	+	+	-	+	-	-	-	-	H	3
<i>Plectranthus australis</i> R. Br.	-	-	+	-	-	-	-	-	?	4
<i>P. incanus</i> Link	+	-	-	+	-	-	-	-	H	3
<i>P. mollis</i> (Burman) Kuntze	+	-	-	+	-	-	-	-	H	3
Tribe Salviaeae										
<i>Salvia plebeia</i> R. Br.	+	+	-	+	-	-	-	-	H	3
<i>S. santolinifolia</i>	+	-	-	+	-	-	-	-	H	3
Verbenaceae										
Subfamily Verbenoideae										
Tribe Citharexyleae										
<i>Citharexylum subserratum</i> Sw.	-	-	-	+	-	-	-	-	A	2
<i>Duranta plumieri</i> Jacq.	-	-	-	+	+	+	-	-	H	2
Tribe Lantaneae										
<i>Lantana camara</i> L.	+	-	-	+	-	-	-	-	A	2
<i>Lippia lanceolata</i> Michaux	+	+	+	+	-	-	-	+	A	1
<i>Stachytarpheta jamaicensis</i> (L.) M. Vahl	+	-	-	-	-	-	-	-	A	2
Tribe Petreeae										
<i>Petrea volubilis</i> L.	+	-	-	+	-	-	-	-	H	2
Tribe Verbeneae										
<i>Verbena hastata</i> L.	-	-	-	+	-	-	-	-	H	1
<i>V. urticifolia</i> L.	-	-	-	+	-	-	-	-	H	1
<i>V. venosa</i> Gillies & Hooker	+	-	-	+	-	-	-	-	A	2

TABLE 1 (continued).

Species	Stomatal Types								St. Loc.	Ref.
	1	2	3	4	5	6	7	8		
Verbenaceae (continued)										
Subfamily Viticoideae										
Tribe Clerodendreae										
<i>Clerodendrum fragrans</i> R. Br.	+	-	-	+	-	-	-	-	H	2
<i>C. inerme</i> (L.) Gaertner	-	-	-	+	-	+	-	-	H	2
<i>C. phlomoides</i> L.f.	-	-	-	+	-	+	-	-	H	2
<i>C. splendens</i> Don	+	-	-	+	-	-	-	-	H	2
<i>C. umbellatum</i> Poiret	+	-	-	+	-	-	-	-	H	2
<i>Holmskioldia sanguinea</i> Retz.	+	-	-	+	+	-	-	-	H	2
Tribe Viticeae										
<i>Gmelina arborea</i> Roxb.	-	-	-	+	-	-	-	-	H	2
<i>Vitex negundo</i> L.	-	-	-	+	+	-	-	-	H	2

^aDiallelocytic types in Inamdar (1969) and Inamdar and Bhatt (1972) were interpreted from their drawings. Subfamilial classification of Labiatae follows Cantino and Sanders's (1986) circumscription of Erdtman's (1945) subfamilies. Tribal classification within subfamily Nepetoideae follows Bentham (1876), with nomenclature corrected by Sanders and Cantino (1984). Tribe Lamieae is circumscribed as discussed in text. Verbenaceae classification follows Briquet (1895).

^bStomatal types: 1 = diacytic, 2 = diallelocytic-1, 3 = diallelocytic-2, 4 = anomocytic, 5 = anisocytic, 6 = paracytic, 7 = helicocytic, 8 = parallelocytic. +, present; -, absent.

^cStomatal location: A = amphistomatic, H = hypostomatic.

^dReferences: 1 = Abu-Asab, 1984; 2 = Inamdar, 1969; 3 = Inamdar & Bhatt, 1972; 4 = Payne, 1970; 5 = Ramayya & Rao, 1969.

Outer stomatal ledges were present in all genera except *Trichostema*. Stomata were found to be at the same level as the epidermis in 24 species, slightly elevated in 12, and markedly elevated in four. Stomatal position varied within a number of genera and within one species (*Physostegia virginiana*). It is probably of little taxonomic value at the generic level and of none in delimiting suprageneric groups.

Our data do not support the observations of El-Gazzar and Watson (1968, 1970) regarding the stomata of Bentham's tribe Lamieae. These authors (1970, p. 476) maintained that if *Prunella* L., *Cleonia* L., and the North American Melittidinae are excluded, anomocytic stomata "are the rule" in Bentham's "Stachydeae" (Lamieae). This is not the case, however, in the Lamieae that we examined. All 16 investigated species of Bentham's Lamieae (including *Scutellaria* but not the North American Melittidinae) had anomocytic stomata; however, all but one also had diacytic stomata, and 12 of them had diallelocytic stomata as well. In most species in which both diacytic and anomocytic stomata were found, the former type was more abundant. El-Gazzar and Watson's (1970) generalization about Bentham's Lamieae thus appears to be incorrect. (On the other hand, anomocytic stomata are at least present in all examined Lamieae except three genera of North American Melittidinae.) Our data also disagree with regard to particular genera in table 1 of El-Gazzar and Watson (1968). They included *Ajuga*, *Galeobdolon*, *Teucrium* L., and most species of *Pogostemon* Desf., *Scutellaria*, and *Stachys* L. in their list of taxa whose stomata

TABLE 2. Stomatal characters in Labiatae examined.^a

Taxa	Stomatal Types ^b						St. Loc. ^c	Ldg. ^d	St. Pos. ^e
	1	2	3	4	5	6			
Subfamily Lamioideae									
Tribe Lamieae									
Subtribe Melittidinae									
<i>Brazoria arenaria</i>	+	+	-	-	-	-	A	+	b
<i>B. pulcherrima</i>	+	+	-	-	-	-	A	+	a
<i>B. scutellarioides</i>	+	+	+	-	-	-	A	+	a
<i>B. truncata</i>	+	+	-	-	-	-	A	+	a
<i>Chelonopsis forrestii</i>	-	-	-	+	-	-	H	+	a
<i>C. moschata</i>	+	-	-	+	-	-	H	+	a
<i>Macbridea alba</i>	+	+	+	-	-	-	A	+	a
<i>M. caroliniana</i>	+	+	+	-	-	-	A	+	a
<i>Melittis melissophyllum</i>	+	+	-	+	-	+	H	+	a
<i>Physostegia angustifolia</i>	+	+	+	-	-	-	A	+	b
<i>P. digitalis</i>	-	+	+	-	-	-	A	+	b
<i>P. godfreyi</i>	+	+	-	-	-	-	A	+	b
<i>P. leptophylla</i>	+	+	+	-	-	-	A	+	a
<i>P. longisepala</i>	-	+	+	-	-	-	A	+	b
<i>P. purpurea</i>	+	+	+	-	-	-	A	+	a
<i>P. virginiana</i>									
subsp. <i>praemorsa</i>	+	+	+	-	-	-	A	+	a
subsp. <i>virginiana</i>	-	+	+	-	-	-	A	+	b
<i>Synandra hispidula</i>	+	+	-	+	-	-	A	+	a
Other Lamieae									
<i>Galeobdolon luteum</i>	+	+	+	+	-	-	H	+	a
<i>Lamium purpureum</i>	+	+	-	+	-	-	A	+	a
<i>Leonurus cardiaca</i>	+	-	-	+	-	-	H	+	b
<i>Marrubium vulgare</i>	+	-	-	+	-	-	A	+	b
<i>Stachys riddellii</i>	+	+	-	+	-	-	H	+	b
<i>S. tenuifolia</i>	+	+	-	+	-	-	H	+	a
Other Lamioideae									
<i>Ajuga reptans</i>	+	+	-	+	-	-	A	+	b
<i>Pogostemon cablin</i>	-	+	-	-	-	-	H	+	a
<i>Prostanthera rotundifolia</i>	+	-	-	+	+	+	A	+	a
<i>Scutellaria elliptica</i>	+	+	+	+	-	-	H	+	a
<i>S. incana</i>	+	+	-	+	-	-	H	+	c
<i>S. integrifolia</i>	+	+	-	+	-	-	A	+	b
<i>S. lateriflora</i>	+	+	-	+	-	-	H	+	a
<i>S. nervosa</i>	+	+	-	+	-	-	H	+	a
<i>S. ovata</i>	+	+	+	+	-	-	H	+	a
<i>S. serrata</i>	+	+	-	+	-	-	H	+	a
<i>Teucrium canadense</i>	+	+	-	+	-	-	H	+	c
<i>T. chamaedrys</i>	+	-	-	+	-	-	H	+	c
<i>Trichostema dichotomum</i>	-	-	-	+	+	+	A	-	a
<i>T. lanceolatum</i>	+	-	-	+	+	+	A	-	a
Subfamily Nepetoideae									
<i>Blephilia hirsuta</i>	+	+	-	+	-	-	H	+	b
<i>Monarda fistulosa</i>	-	+	-	-	-	-	H	+	c

^aSubfamilial classification follows Cantino and Sanders's (1986) circumscription of Erdtman's (1945) subfamilies. Tribe Lamieae is circumscribed as discussed in text.

^bStomatal types: 1 = diacytic, 2 = diallelocytic-1, 3 = diallelocytic-2, 4 = anomocytic, 5 = anisocytic, 6 = paracytic.

^cStomatal location: A = amphistomatic, H = hypostomatic.

^dLdg. = outer ledges: +, present; -, absent.

^eStomatal position: a = level with the epidermis, b = slightly elevated, c = strongly elevated.

are predominantly anomocytic and/or anisocytic. We found the stomata of all of these genera to be predominantly to entirely diacytic and/or diallelocytic.

TRICHOMES

NONGLANDULAR TRICHOMES. Simple, uniseriate trichomes were found on the leaves of most species. Only *Physostegia* (all species examined), *Macbridea* (both species), and *Prostanthera rotundifolia* lacked nonglandular foliar trichomes and could be described as having glabrous leaves if the minute, subsessile glands were ignored (see below). Of these three genera, only *Physostegia* consistently has glabrous leaves (Cantino, 1982). Species of *Prostanthera* not examined in this study have pubescent leaves (Conn, 1984), as do some individuals of both *Macbridea alba* (Godfrey & Wooten, 1981; Kral, 1983) and *M. caroliniana* (Godfrey & Wooten, 1981). The leaves of *Brazoria* are nearly glabrous, with the usually sparse trichomes concentrated toward the base of the blade (the leaves of *B. scutellarioides* are essentially glabrous throughout).

The only other nonglandular trichomes observed were dendritic in form and confined to *Marrubium vulgare*. These are stalked and basally branched, with the stalk composed of several cells, a ray arising from each stalk cell, and each ray composed of one to six cells. Similar trichomes were reported by Solereder (1908) and Theobald and colleagues (1979) from other species of *Marrubium* and were illustrated in the latter publication.

The simple trichomes vary in cell number (see TABLE 3). Unicellular trichomes were found in eight genera and 12 species, while multicellular ones were observed in all species. The variation in cell number may prove on further study to be of taxonomic use within genera or in distinguishing among closely related genera, but it appears to be of no value in delimiting suprageneric taxa in the Labiatae.

GLANDULAR TRICHOMES. Two distinct classes of glandular trichomes were observed. Clavate glandular trichomes (see FIGURE 2), found in 14 species, consist of a unicellular or multicellular head resting on a relatively long, multicellular, uniseriate stalk, the uppermost cell of which is usually discoid. Subsessile glandular trichomes (see FIGURE 3), found in nearly all species, consist of a unicellular or multicellular head borne on one (rarely two) short, discoid stalk cell(s) resting on one or more foot cells. The foot cells are generally sunken below the level of the adjacent epidermis, the gland as a whole lying in a tiny depression on the leaf surface. The cuticle is fused to the wall of the stalk cell but appears to separate from the wall of the head, leaving a space in which secretions accumulate. (For excellent photographs, plus evidence that the separated cuticle is provided with a noncellulosic framework derived from the outermost wall layer of the head cells, see Bruni & Modenesi, 1983.)

There is considerable variation in size and morphology of clavate glandular trichomes (see FIGURE 2). Those of *Synandra hispidula* and the four species of *Scutellaria* in which clavate glandular trichomes were observed (*S. elliptica*, *S. nervosa*, *S. ovata*, and *S. serrata*) are quite similar, with a four-celled head atop a more or less discoid stalk cell, and three to six elongate stalk cells. Clavate

TABLE 3. Simple, nonglandular trichomes in Labiatae examined.^a

Species	Trichomes ^b			
	1	2	3	4
Subfamily Lamioideae				
Tribe Lamieae				
Subtribe Melittidinae				
<u>Brazoria arenaria</u>	-	+	+	+
<u>B. pulcherrima</u>	-	+	+	-
<u>B. scutellarioides</u>	+	+	-	-
<u>B. truncata</u>	-	+	+	+
<u>Chelonopsis forrestii</u>	-	+	+	-
<u>C. moschata</u>	-	-	+	+
<u>Melittis melissophyllum</u>	-	+	+	+
<u>Synandra hispidula</u>	-	+	+	+
Other Lamieae				
<u>Galeobdolon luteum</u>	-	+	+	+
<u>Lamium purpureum</u>	+	+	-	-
<u>Leonurus cardiaca</u>	-	+	+	-
<u>Marrubium vulgare</u>	-	+	+	+
<u>Stachys riddellii</u>	+	+	-	-
<u>S. tenuifolia</u>	+	+	-	-
Other Lamioideae				
<u>Ajuga reptans</u>	-	+	+	+
<u>Pogostemon cablin</u>	-	+	+	+
<u>Scutellaria elliptica</u>	-	+	+	+
<u>S. incana</u>	+	+	+	+
<u>S. integrifolia</u>	+	+	+	-
<u>S. lateriflora</u>	-	+	+	+
<u>S. nervosa</u>	+	+	+	+
<u>S. ovata</u>	-	+	+	+
<u>S. serrata</u>	-	+	+	+
<u>Teucrium canadense</u>	-	+	+	+
<u>T. chamaedrys</u>	+	+	+	+
<u>Trichostema dichotomum</u>	+	+	+	+
<u>T. lanceolatum</u>	+	+	+	+
Subfamily Nepetoideae				
<u>Blephilia hirsuta</u>	+	+	+	+
<u>Monarda fistulosa</u>	+	+	+	+

^aSpecies with glabrous leaves omitted; see text. Classification of suprageneric taxa as in TABLE 2.

^bTypes of trichomes: 1, one-celled; 2, two-celled; 3, three-celled; 4, with more than three cells; +, present; -, absent.

trichomes with heads composed of more than four cells were found only in *Brazoria truncata* and *B. scutellarioides* but resemble those on the calyx and inflorescence axis in *Physostegia* (Cantino, 1979, 1982). Clavate trichomes with single-celled heads were observed in *Marrubium vulgare* and *Trichostema lanceolatum*.

Subsessile glandular trichomes are very characteristic of the Labiatae and occur in many Verbenaceae as well (Solereeder, 1908; Metcalfe & Chalk, 1950). They have been referred to by a variety of names, including shortly-stalked bladder-like glands (Metcalfe & Chalk, 1950), sunken glandular dots (Huang & Cheng, 1971), glandular scales (Bosabalidis & Tsekos, 1982), and glandular capitate sessile trichomes (Shah & Naidu, 1983). The term subsessile seems appropriate to us since the glands appear to be sessile unless examined very closely. Because of their nearly universal occurrence in the Labiatae and the extensive variation in their complexity, subsessile glandular trichomes offer considerable potential as a taxonomic character in the family. They have been little used for this purpose, perhaps in part due to lack of a satisfactory classification of the glands on which to base taxonomic comparisons. We have developed such a classification (see APPENDIX 2), based on number of cells and cell-wall configurations (FIGURE 4) in the head of the gland.

Terms used to describe cell-wall configurations are adopted from Stace (1973). A primary radial wall originates from the center of the head of a gland and ends at the periphery. A secondary radial wall originates on a primary radial wall and ends at the periphery. A tertiary radial wall originates on a secondary radial wall and ends at the periphery. A tangential wall connects two radial walls. A partial radial wall originates on a tangential wall and ends at the periphery.

Subsessile glandular trichomes (see FIGURE 5) were found on the leaves of all species examined except *Trichostema lanceolatum* (see TABLE 4). Gland types 4 and 5 were encountered in nearly all species, both within and outside of subtribe Melittidinae. Types 2 and 3 are rare and type 1 absent in the Melittidinae. Type 1 was found only in *Pogostemon*, while type 2 was commonest in *Teucrium* and *Pogostemon*.

The more complex gland types (6–10) were most frequently encountered in *Scutellaria* and the North American Melittidinae. Glands with partial radial walls (types 7 and 10) were restricted to subtribe Melittidinae, where they were found in all species of *Brazoria*, *Macbridea*, and *Synandra*, as well as in two species of *Physostegia*. Type 7 was found only in *Synandra*. The systematic value of the complex gland types in subtribe Melittidinae is discussed below.

LEAF HISTOLOGY

All species examined have a uniseriate epidermis composed of unsclerified, thin-walled cells and a midrib consisting of an arcuate collateral bundle; all lack a hypodermis. Of the other characters investigated, two (number of cell layers in palisade parenchyma and shape of palisade cells) are too variable on individual specimens to be of any taxonomic use. Histological characters that

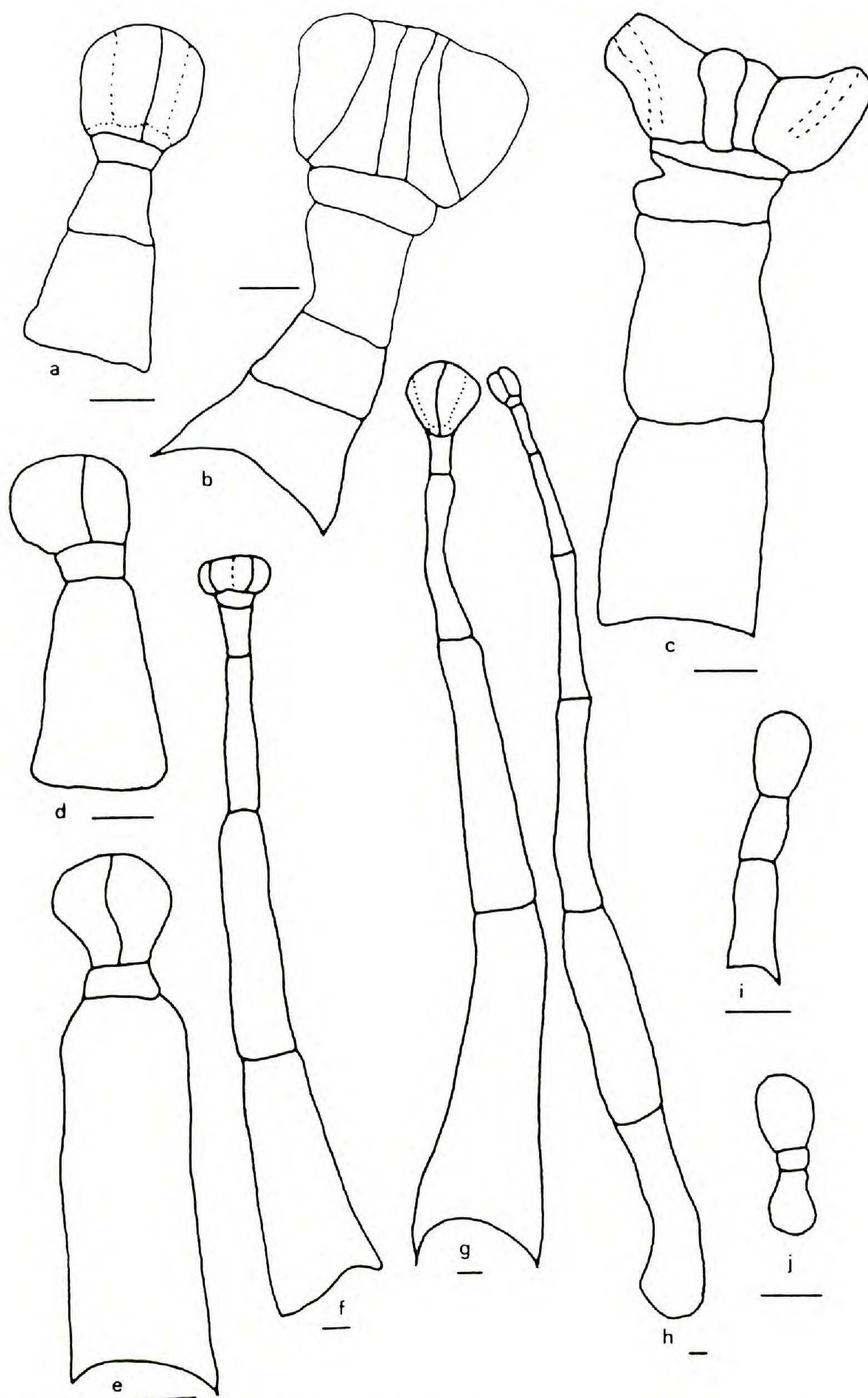


FIGURE 2. Clavate glandular trichomes: a, *Brazoria arenaria*; b, *B. scutellarioides*; c, *B. truncata*; d, *Melittis melissophyllum*; e, *Stachys riddellii*; f, *Synandra hispidula*; g, *Scutellaria nervosa*; h, *S. elliptica*; i, *Trichostema lanceolatum*; j, *Marrubium vulgare*. Scale bars = 15 μ m.

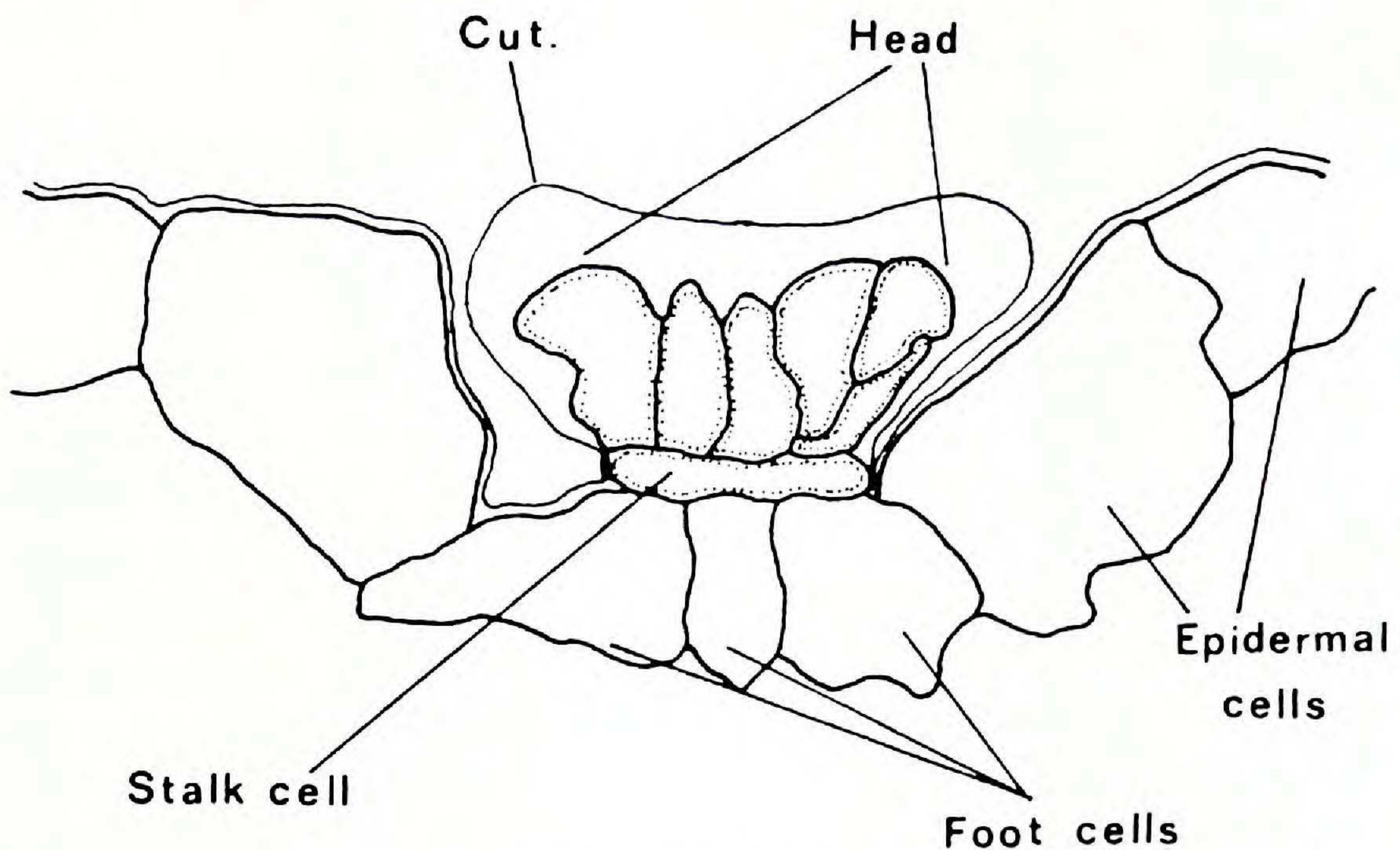


FIGURE 3. Subsessile glandular trichome (*Macbridea alba*), transverse section. Cut. = cuticle.

may be of some taxonomic value are listed in APPENDIX 3, and the distribution of their character states is summarized in TABLE 5.

Most of these characters vary too much within genera to be of much value in circumscribing suprageneric groups. They may prove useful, however, in distinguishing species or species groups within certain genera (i.e., characters 2 and 6 in *Brazoria*; 1, 2, 4, 5, 6, and 7 in *Physostegia*; 2 and 4 in *Scutellaria*; and 1 in *Trichostema*). A much more extensive sample will be necessary before even tentative conclusions can be drawn at this taxonomic level.

In the assessment of phylogenetic relationships above the genus level, presence of idioblasts in the mesophyll appears to be the character with the greatest potential because it varies among but not within genera. Two kinds of idioblasts were observed. One of them, seen only in *Pogostemon*, resembles a glandular trichome but occurs inside the leaf (FIGURE 6h). These structures were also noted by Solereder (1908, p. 1022), who described them as "internal glandular hairs" provided with a short stalk of two or three suberized cells and a unicellular, cuticularized head projecting into the intercellular spaces. He also noted that a secretion accumulates under the cuticle, which is raised like a bladder, just as in an external trichome.

The second kind of idioblast is a large, saclike cell, presumably secretory in function (FIGURE 6a-g). These were observed in all species of *Brazoria* and all investigated species of *Physostegia*. They were also noted by Solereder (1908) in *Physostegia intermedia*, a species that we did not examine. Our observations and those of Solereder suggest that within the Lamiales such saclike idioblasts are unique to these two genera. They vary in shape and thus may offer a good

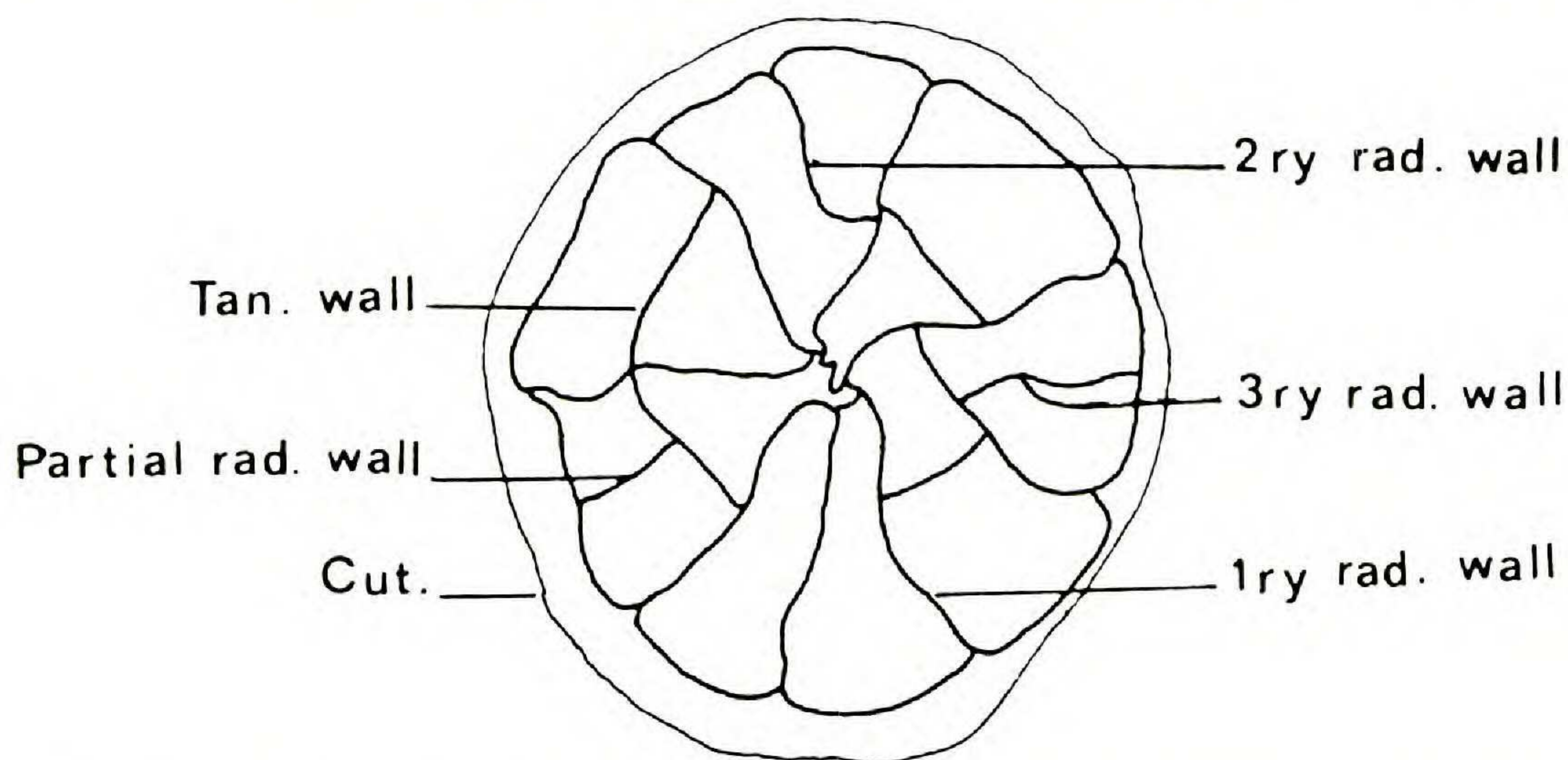


FIGURE 4. Subsessile glandular trichome, surface view, showing cell-wall configurations in head. Cut. = cuticle, tan. = tangential, rad. = radial. (Adapted from Stace, 1973.)

taxonomic character at the species level, in addition to providing evidence for a close relationship between *Physostegia* and *Brazoria*.

DISCUSSION

Discussion will center on the question of whether leaf anatomy provides evidence for the monophyly of subtribe Melittidinae as a whole and/or of subgroups within it. The existence of shared, derived character states (synapomorphies) would constitute such evidence (Hennig, 1966; Wiley, 1981).

The identification of synapomorphies is a two-step procedure. First, an evolutionary transformation series (Wiley, 1981) is hypothesized for each character, usually on the basis of ontogeny and structural complexity of the character states. (This step is trivial when the character is binary.) Second, the evolutionary polarity of the characters must be assessed. Of the many criteria that have been used to determine polarity (see review by Stevens, 1980), outgroup comparison is now the most widely accepted (see, for example, Eldredge & Cracraft, 1980; Stevens, 1980; Arnold, 1981; Wiley, 1981; Farris, 1982) and is the sole criterion used here. Outgroup comparison, in its simplest form, can be explained as follows: "For a given character with 2 or more states within a group, the state occurring in related groups [the outgroups] is assumed to be the plesiomorphic state" (Watrous & Wheeler, 1981). (For a thorough discussion of the underlying logic of outgroup comparison, which is based on the principle of parsimony, see Maddison *et al.*, 1984.)

Because the monophyly of the Melittidinae is in question, the ingroup must be a demonstrably monophyletic group that includes (but is not limited to) this subtribe. The least-inclusive such group is tribe Lamieae, as circumscribed above (i.e., Bentham's tribes Lamieae and Prasieae minus *Anisomeles*, *Scutellaria*, and probably *Salazaria*; see "Taxonomic Background" for evidence

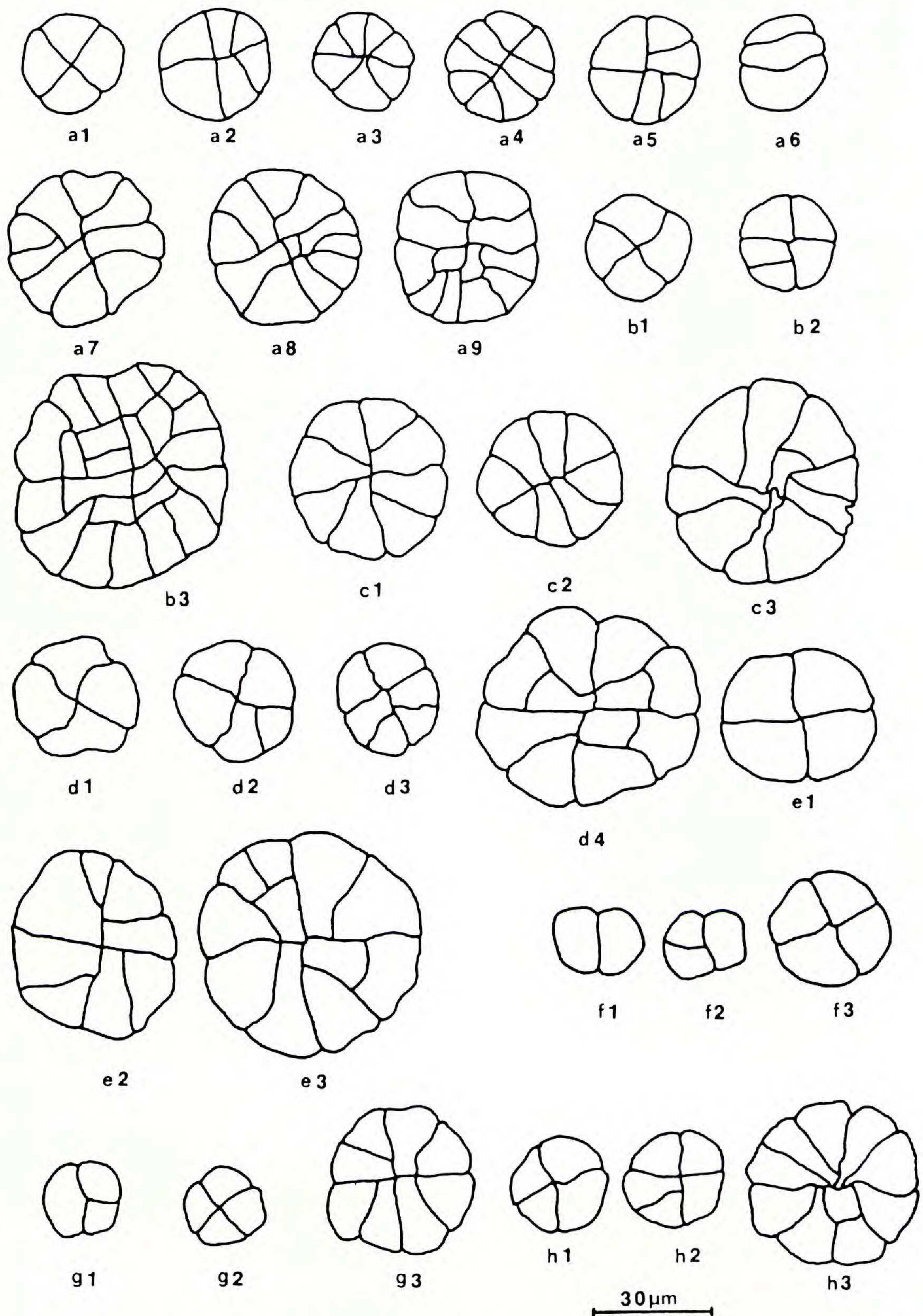


FIGURE 5. Subsessile glandular trichomes, surface view: a1-a9, *Brazoria arenaria*; b1-b3, *Physostegia virginiana* subsp. *praemorsa*; c1-c3, *Macbridea alba*; d1-d4, *M. caroliniana*; e1-e3, *Synandra hispidula*; f1-f3, *Teucrium canadense*; g1-g3, *Marrubium vulgare*; h1-h3, *Scutellaria incana*.

TABLE 4. Distribution of sessile glandular trichomes.^a

Taxa	Trichomes ^b									
	1	2	3	4	5	6	7	8	9	10
Subfamily Lamioideae										
Tribe Lamieae										
Subtribe Melittidinae										
<u>Brazoria arenaria</u>	-	-	a	+	+	-	-	+	+	+
<u>B. pulcherrima</u>	-	-	-	+	+	-	-	+	+	+
<u>B. scutellarioides</u>	-	-	-	+	+	+	-	-	+	+
<u>B. truncata</u>	-	-	-	+	+	-	-	+	+	+
<u>Chelonopsis forrestii</u>	-	+	-	+	+	-	-	-	-	-
<u>Macbridea alba</u>	-	-	-	+	+	+	-	+	+	+
<u>M. caroliniana</u>	-	-	-	+	+	+	-	-	+	+
<u>Melittis melissophyllum</u>	-	-	-	+	+	-	-	-	-	-
<u>Physostegia angustifolia</u>	-	-	-	+	+	-	-	+	+	+
<u>P. digitalis</u>	-	-	-	+	+	-	-	-	-	-
<u>P. godfreyi</u>	-	-	-	+	+	-	-	+	-	-
<u>P. leptophylla</u>	-	-	-	+	+	+	-	-	-	-
<u>P. longisepala</u>	-	-	-	+	+	-	-	-	-	-
<u>P. purpurea</u>	-	-	-	+	+	-	-	-	-	-
<u>P. virginiana</u>										
subsp. <u>praemorsa</u>	-	-	-	+	+	-	-	-	+	+
subsp. <u>virginiana</u>	-	-	-	+	+	-	-	-	-	+
<u>Synandra hispidula</u>	-	-	-	+	+	+	+	-	+	-
Other Lamieae										
<u>Galeobdolon luteum</u>	-	-	-	+	+	+	-	-	+	-
<u>Lamium purpureum</u>	-	+	b	+	+	+	-	-	-	-
<u>Leonurus cardiaca</u>	-	+	b	+	+	+	-	+	+	-
<u>Marrubium vulgare</u>	-	+	b	+	+	-	-	-	-	-
<u>Stachys riddellii</u>	-	-	-	+	+	-	-	-	-	-
<u>S. tenuifolia</u>	-	-	-	+	+	-	-	-	-	-
Other Lamioideae										
<u>Ajuga reptans</u>	-	+	-	+	-	-	-	-	-	-
<u>Pogostemon cablin</u>	+	+	-	-	-	-	-	-	-	-
<u>Prostanthera rotundifolia</u>	-	-	b	+	-	-	-	+	-	-
<u>Scutellaria elliptica</u>	-	-	-	+	-	-	-	+	-	-
<u>S. incana</u>	-	-	-	+	+	+	-	+	+	-
<u>S. integrifolia</u>	-	-	-	+	+	-	-	+	-	-
<u>S. lateriflora</u>	-	+	b	+	+	-	-	-	-	-
<u>S. nervosa</u>	-	-	-	+	+	-	-	+	-	-
<u>S. ovata</u>	-	-	b	+	+	+	-	+	-	-
<u>S. serrata</u>	-	+	b	+	+	-	-	-	-	-
<u>Teucrium canadense</u>	-	+	b	+	+	-	-	-	-	-
<u>T. chamaedrys</u>	-	+	b	+	-	-	-	-	-	-
<u>Trichostema dichotomum</u>	-	-	b	+	-	-	-	-	-	-
Subfamily Nepetoideae										
<u>Blephilia hirsuta</u>	-	-	-	-	+	-	-	-	-	-
<u>Monarda fistulosa</u>	-	-	-	-	+	-	-	-	-	-

^aClassification of suprageneric taxa as in TABLE 2.

^bNumbers (1-10) and letters (a, b) refer to trichome classification in APPENDIX 2; +, present; -, absent.

TABLE 5. Leaf histological characters as recorded from transverse sections.

Taxa	Characters ^b						
	1	2	3	4	5	6	7
Subfamily Lamioideae							
Tribe Lamieae							
Subtribe Melittidinae							
<u>Brazoria arenaria</u>	b	b	b	a	a	b	b
<u>B. pulcherrima</u>	b	b	b	a	a	c	b, e
<u>B. scutellarioides</u>	b	a	b	a	a	b	b
<u>B. truncata</u>	b	b	b	a	a	a	b
<u>Chelonopsis forrestii</u>	b	a	a	a	a	c	e
<u>Macbridea alba</u>	b	a	a	a	a	b	a
<u>M. caroliniana</u>	b	a	a	a	c	c	e
<u>Melittis melissophyllum</u>	b	a	a	a	a	c	e
<u>Physostegia angustifolia</u>	b	a	b	d	a	c	c
<u>P. digitalis</u>	b	a	b	d	a	a	c
<u>P. godfreyi</u>	a	a	b	d	a	a	a
<u>P. leptophylla</u>	b	a	b	a	a	a	b
<u>P. longisepala</u>	b	b	b	a	b	a	b
<u>P. purpurea</u>	b	a	b	d	a	a	b
<u>P. virginiana</u>							
subsp. <u>praemorsa</u>	b	a	b	d	a	c	b
subsp. <u>virginiana</u>	b	a	b	b?	a	c	e
<u>Synandra hispidula</u>	b	b	a	a	a	c	e
Other Lamieae							
<u>Galeobdolon luteum</u>	b	b	a	a	a	c	e
<u>Lamium purpureum</u>	b	a	a	a	a	c	d
<u>Leonurus cardiaca</u>	b	a	a	a	c	c	e
<u>Marrubium vulgare</u>	b	a	a	a	b	c	e
<u>Stachys riddellii</u>	b	a	a	a	b	c	e
<u>S. tenuifolia</u>	b	a	a	a	b	c	e
Other Lamioideae							
<u>Ajuga reptans</u>	b	a	a	a	a	b	d
<u>Pogostemon cablin</u>	b	a	c	a	a	c	e
<u>Prostanthera rotundifolia</u>	b	a	a	a	a	a	a
<u>Scutellaria elliptica</u>	b	b	a	a	a	c	e
<u>S. incana</u>	b	a	a	a	a	c	e
<u>S. integrifolia</u>	b	a	a	a	a	c	d
<u>S. lateriflora</u>	b	b	a	a	a	c	e
<u>S. nervosa</u>	b	b	a	c	a	c	d
<u>S. ovata</u>	b	a	a	a	a	c	e
<u>S. serrata</u>	b	b	a	a	a	c	d
<u>Teucrium canadense</u>	b	a	a	a	a	c	e
<u>T. chamaedrys</u>	b	a	a	a	a	c	d
<u>Trichostema dichotomum</u>	b	a	a	a	a	b	d
<u>T. lanceolatum</u>	c	a	a	a	a	c	d
Subfamily Nepetoideae							
<u>Blephilia hirsuta</u>	b	a	a	a	a	c	e
<u>Monarda fistulosa</u>	b	a	a	a	a	c	e

^aClassification of suprageneric taxa as in TABLE 2.

^bCharacters explained in APPENDIX 3.

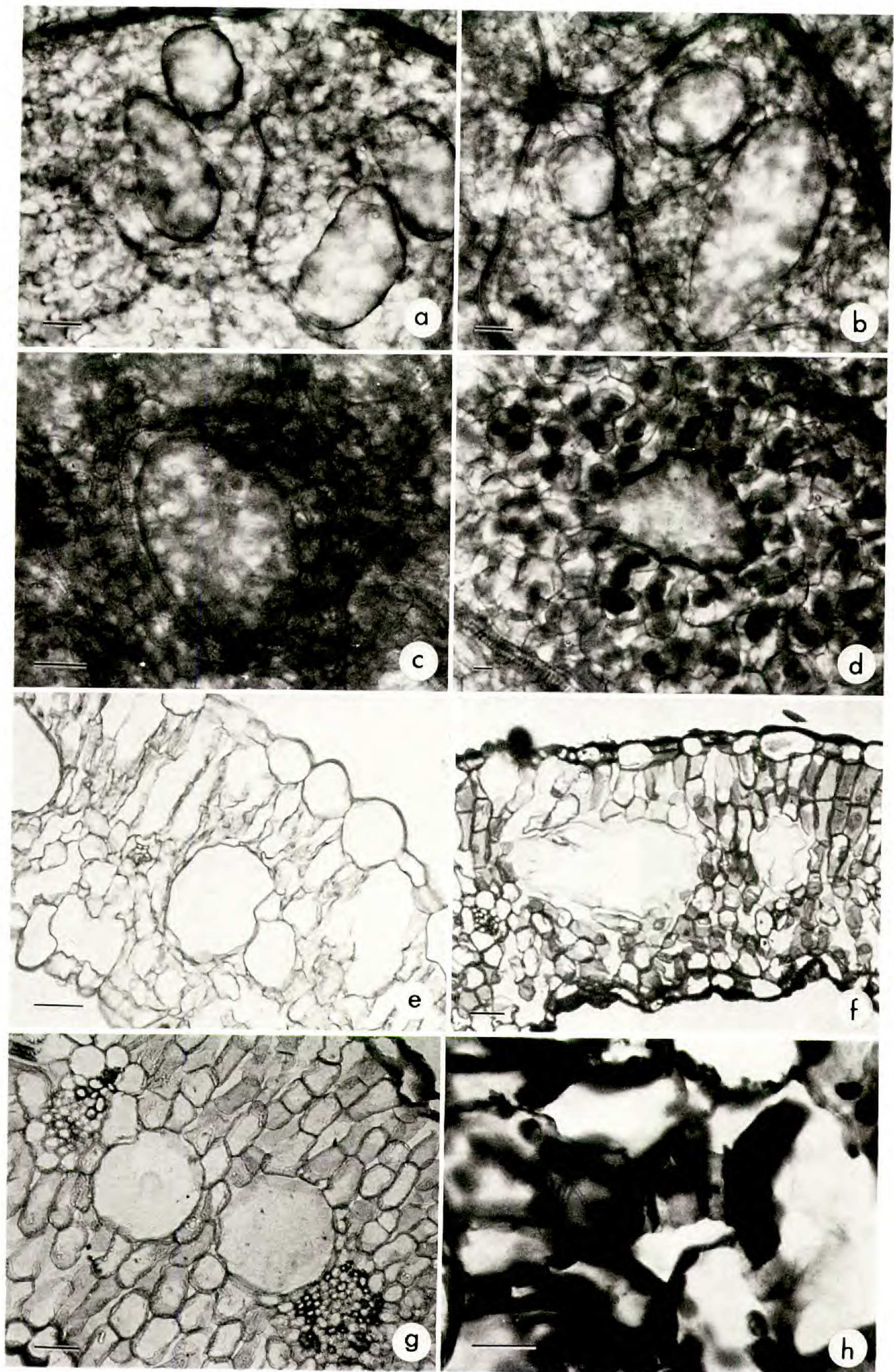


FIGURE 6. Idioblasts in mesophyll. a-d, saclike idioblasts, surface view: a, *Brazoria arenaria* (Kessler 5771); b, *Brazoria pulcherrima* (Kessler 5862); c, *Physostegia godfreyi* (Cantino 1054); d, *Physostegia leptophylla* (Cantino 971). e-g, saclike idioblasts, trans-

supporting the monophyly of this group). The ingroup is represented in our study by all six genera of subtribe Melittidinae plus five others (*Galeobdolon*, *Lamium*, *Leonurus* L., *Marrubium*, and *Stachys*). Anatomical data for two additional genera (*Phlomis* and *Eremostachys*) have been provided by Azizian and Cutler (1982). For stomatal characters the ingroup sample includes *Leontotis* (Pers.) R. Br. and *Leucas*, as well (Inamdar & Bhatt, 1972).

Choice of outgroups is constrained by both the uncertainty about cladistic relationships within the family and the paucity of anatomical data for the Labiatae. We have selected as outgroups those few non-ingroup taxa of subfamily Lamioideae for which we have collected anatomical data (*Ajuga reptans*, *Pogostemon cablin*, *Prostanthera rotundifolia*, *Scutellaria* [7 spp.], *Teucrium* [2 spp.], and *Trichostema* [2 spp.]), plus subfamily Nepetoideae as a whole. The latter must be included because, as discussed above, there is no evidence that subfamily Lamioideae is monophyletic. If it were paraphyletic by exclusion of subfamily Nepetoideae, the latter might be more closely related to tribe Lamieae (the ingroup) than are some of the other selected outgroups. Subfamily Nepetoideae is represented by our own data for *Monarda fistulosa* and *Blephilia hirsuta* and by published data for *Zhumeria* Rech. f. & Wendelbo (Bokhari & Hedge, 1976), tribe Meriandreae (Bokhari & Hedge, 1971), and subtribe Hyp-tidinae (Rudall, 1979, 1980). For stomatal characters (see TABLE 1) ten other genera can be added as representatives of subfamily Nepetoideae, two other species can be added as representatives of *Pogostemon*, and *Dysophylla* Blume and *Anisomeles* can be added to the list of outgroups. For sessile glands, nine other genera can be added as representatives of subfamily Nepetoideae (Bruni & Modenesi, 1983; Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985). Each of the outgroups is thought to be monophyletic, and no two of them can be combined into a more inclusive monophyletic group. For example, there is no evidence that tribe Ajugeae *sensu* Bentham, represented in this study by *Ajuga*, *Teucrium*, and *Trichostema*, is monophyletic.

The outgroups must be used in combination, because even the more distant outgroups may affect polarity assessment in the ingroup (Maddison *et al.*, 1984). The analysis is complicated, however, by the lack of resolution of phylogenetic relationships among the outgroups and by uncertainty about which outgroups are most closely related to the ingroup. If a state that occurs in the ingroup occurs in none of the outgroups, it is clearly derived within the ingroup, but if it occurs in some outgroup taxa (the most frequent situation), polarity assessment is more problematic. The outgroup-substitution approach (Donoghue & Cantino, 1984) is applicable to this situation but difficult to apply here because of the large number of plausible outgroup combinations that must be considered. Moreover, both this approach and the global parsimony approach of Maddison and colleagues (1984) require a full cladistic analysis using all

verse section: e, *Brazoria pulcherrima* (Kessler 5865); f, *Physostegia angustifolia* (Cantino 1058); g, *Physostegia godfreyi* (Cantino 1054). h, internal glandular trichome, transverse section, *Pogostemon cablin* (Cantino 1262). Scale bars = 60 μm (a-g) and 20 μm (h).

available characters, whereas the intent here is simply an evaluation of the possible phylogenetic significance of a few specific characters.

An alternative method will therefore be used to evaluate polarity of characters that vary within the outgroups. This approach, developed by Frohlich (1983, 1987), involves calculation of the probability that the commonest state among the outgroups could parsimoniously be treated as ancestral in the ingroup if the cladistic relationships of the outgroups to each other and to the ingroup were known. Frohlich has developed an algorithm that considers all possible arrangements of the outgroups, determines for each arrangement which state of a binary character it is most parsimonious to consider as ancestral within the ingroup, and then calculates the percentage of arrangements that assign each state as ancestral in the ingroup. This can be converted to probability if all outgroup combinations are assumed to be equally probable, a necessary assumption when one is ignorant of the true outgroup relationships. Thus, according to Frohlich, if a state occurs in only one of seven outgroups, the probability is 0.909 that the alternative state could parsimoniously be treated as ancestral within the ingroup if outgroup relationships were known (i.e., 90.9% of the outgroup arrangements yield this polarity assessment, while the rest yield an equivocal one). Frohlich's "tree-count method" turns out to be helpful in determining the polarity of several characters (see below).

A derived character state that occurs in some, but not all, members of a monophyletic group is called a nonuniversal derived state (Cantino, 1985b). A nonuniversal derived state shared by two or more groups, each known to be monophyletic on the basis of other characters, provides evidence that these groups together constitute a clade, but it is weaker evidence than if monophyly is inferred on the basis of a synapomorphy that occurs in all members of the clade it delimits (Cantino, 1985b). Both synapomorphies and shared nonuniversal derived states are used in the following analysis.

TRANSFORMATION SERIES

Most characters examined in this study are binary. Of the multistate characters only two, stomatal type and sessile glandular trichomes, display variation of phylogenetic significance at the suprageneric level.

Based on ontogenetic studies (see FIGURE 1), a transformation series for stomatal types is proposed (FIGURE 7a). The anomocytic type is the simplest ontogenetically. The diacytic and diallelocytic stomata form a transformation series from the anomocytic type. The anisocytic and paracytic types, which form a second transformation series from the anomocytic type, share the initial step in their ontogenies (FIGURE 1) but diverge after that point.

Bosabalidis and Tsekos (1984) studied the ontogeny of sessile glandular trichomes in *Origanum* L. They found that a single initial protodermal cell divides to give in succession what we have called trichome types 2, 4, 5, and 6. Based on this study, as well as on a comparison of the structural complexity of the mature trichomes, a transformation series for the sessile glandular trichomes is hypothesized (FIGURE 7b). Type 1 is the simplest structurally and ontogenetically, while type 10 is the most complex. Tangential walls occur in the heads of types 6, 7, 9, and 10. Partial radial walls occur only in types 7

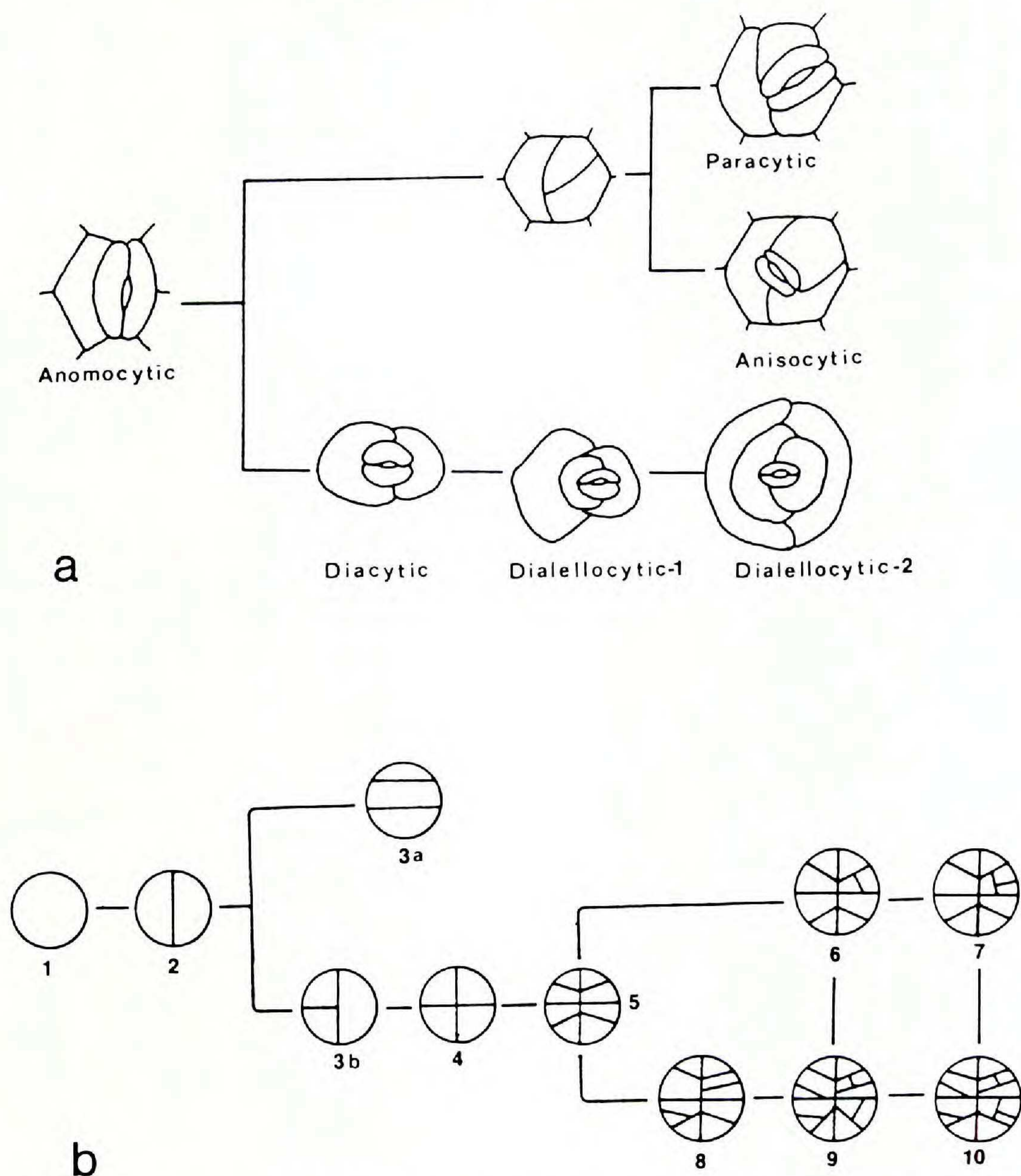


FIGURE 7. Hypothesized transformation series: a, stomatal types; b, subsessile glandular trichomes.

and 10. Types 5, 6, and 7 differ from types 8, 9, and 10 in that the former have no more than one secondary radial wall on a given side of any primary radial wall and lack tertiary radial walls, while the latter have more than one secondary radial wall on a given side of at least one primary radial wall and/or have tertiary radial walls. Types 9 and 10 trichomes can develop by more than one ontogenetic pathway and are therefore not necessarily homologous in all taxa in which they occur.

CHARACTER POLARITY

Anomocytic and diacytic stomata are widely distributed in both the Verbenaceae and the Labiatae (see TABLES 1, 2). Dialellocytic-1 stomata are wide-

spread among the Labiatae, including the outgroups to tribe Lamieae. Diallelocytic-2 stomata are known to occur in four genera of tribe Lamieae plus four species among the outgroups (*Scutellaria elliptica*, *S. ovata*, *Ocimum basilicum*, and *Plectranthus australis*). Both diallelocytic types appear to be rare in the Verbenaceae. The anisocytic and paracytic types occur mainly in the Verbenaceae and the primitive Labiatae (i.e., tribes Prostanthereae and Ajugeae).

The above distribution suggests that although both diallelocytic types are probably derived within the Labiatae, the diallelocytic-1 type is plesiomorphic in tribe Lamieae. Based on Frohlich's (1987) probability table, there is a probability of over 0.984 that the diallelocytic-2 type can parsimoniously be hypothesized to be derived within tribe Lamieae. This calculation is based on its occurrence in two of the seven examined species of one outgroup (*Scutellaria*) and in two of the four examined species of another (subfam. Nepetoideae), and on its absence from the other five outgroups. The many other species of subfam. Nepetoideae in TABLE 1 (in none of which were diallelocytic-2 stomata reported) are ignored in this analysis because the sample for each consisted only of published drawings. If these species were to be included, the probability that the diallelocytic-2 type is derived in the Lamieae would be even greater.

Among the sessile glandular trichomes (see TABLE 4), types 4 and 5 are common throughout the Labiatae and thus plesiomorphic within tribe Lamieae. Types 1, 2, and 3b are of scattered occurrence but apparently do not occur in the North American Melittidinae. Of the more complex glands, types 6, 8, and 9 appear to be too common in the outgroups, particularly in subfamily Nepetoideae in the case of types 6 and 9 (Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985), to permit polarity assessment in the ingroup. Glands with partial radial walls (types 7 and 10) were found only in the Lamieae, however, where they apparently represent a derived state.

The saclike idioblasts in the mesophyll of *Brazoria* and *Physostegia* appear to be unique to these genera and thus represent a synapomorphy. Undifferentiated mesophyll has been observed only in *Physostegia godfreyi* and may represent an autapomorphy of the species. Bundle-sheath extensions are absent (state a of character 6, TABLE 5) in some Lamieae (one species of *Brazoria* and five of *Physostegia*) but are present in all but one outgroup. Similarly, keels on the secondary veins are absent (states a-c of character 7, TABLE 5) in some Lamieae (*Brazoria* and some species of *Macbridea* and *Physostegia*) but present in all but one outgroup. According to Frohlich's (1987) probability table, there is a 0.909 probability that a state occurring in six of seven outgroups can be parsimoniously hypothesized to be ancestral within the ingroup. If this level of probability is deemed acceptable, absence of bundle-sheath extensions and of secondary-vein keels can tentatively be treated as derived in the Lamieae.

PHYLOGENETIC HYPOTHESES

Since the samples of both ingroup and outgroup taxa are small and only leaf anatomy is being considered, phylogenetic hypotheses must be considered very preliminary. The characters that offer apparent synapomorphies should be

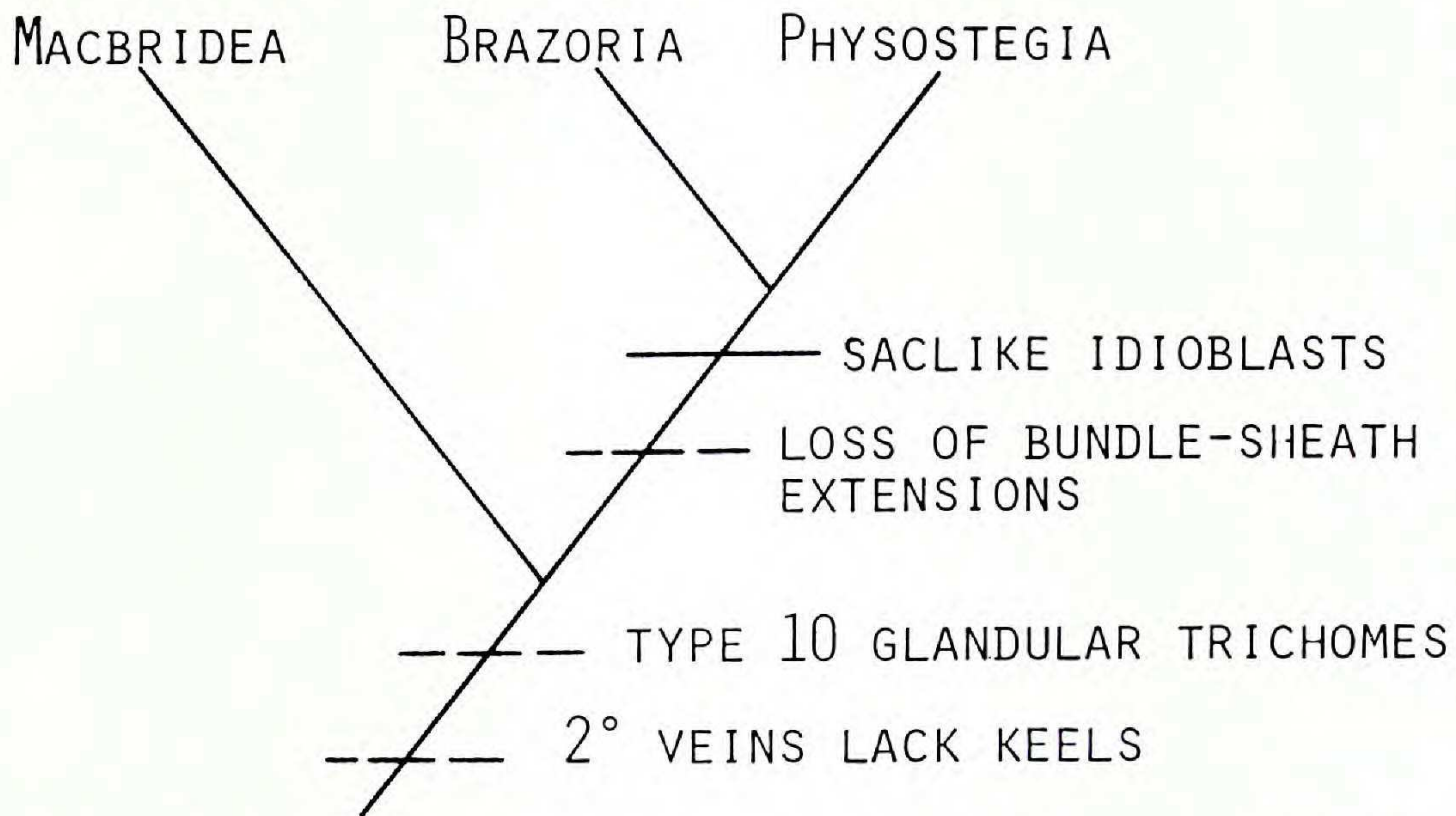


FIGURE 8. Cladogram showing hypothesized phylogenetic relationships between *Brazoria*, *Physostegia*, and *Macbridea*. Solid bar = synapomorphy; dashed bars = shared nonuniversal derived states.

examined in a broader survey of both tribe Lamieae and the outgroups. The latter may force reassessment of character polarity in some cases, while expansion of the ingroup sample may increase the membership of certain clades. Moreover, other sets of characters may support conflicting hypotheses. At the very least, however, this analysis should help focus future investigations on particular characters and taxa.

Shinners (1953) suggested that *Brazoria* and *Physostegia* are close relatives. In the numerical phenetic analysis of El-Gazzar (1969), these two genera paired on the phenogram at a very high similarity level. Until now, however, no strong evidence that they form a monophyletic group (i.e., the occurrence of synapomorphies) has been reported. In the present study an apparent synapomorphy—the occurrence of saclike idioblasts in the mesophyll of all examined species of both genera—has been documented. No other taxon in the Lamiales is known to have this feature. Weaker additional support for the monophyly of this clade is provided by a shared nonuniversal derived state (Cantino, 1985b), absence of bundle-sheath extensions. As discussed above, there is a 0.909 probability that this state can parsimoniously be hypothesized to be derived since it occurs in one of seven outgroups (*Prostanthera*).

Cantino (1982) suggested that *Brazoria*, *Physostegia*, and *Macbridea* may form a monophyletic subgroup within the Melittidinae. No synapomorphy was found to corroborate this hypothesis, but it is supported by two nonuniversal derived states (FIGURE 8). Type 10 glandular trichomes, the most complex sessile glands, occur in all species of *Brazoria* and *Macbridea* and two species of *Physostegia*, but they were not observed in any other taxa of either the ingroup or the outgroup. Weaker additional support for the *Brazoria-Physostegia-Macbridea* clade is provided by another nonuniversal derived state that

occurs in one outgroup as well as in this clade, but nowhere else in the ingroup. Secondary veins lack keels in three species of *Brazoria* (and may or may not lack them in the fourth), *Macbridea alba*, most species of *Physostegia*, and the outgroup species *Prostanthera rotundifolia*. This is probably a reflection of the relatively succulent nature of the leaves of these taxa. As discussed above, there is a 0.909 probability that the loss of secondary-vein keels can be parsimoniously hypothesized to be derived in the ingroup. However, the independent evolution of this character state in the outgroup and ingroup indicates that it may be particularly subject to parallelism, which reduces its value as a phylogenetic indicator (Gosliner & Ghiselin, 1984). If absence of secondary-vein keels is indeed a function of leaf succulence, it can be expected in other succulent Labiatae that have not yet been examined. Such a character state can provide only weak support for the *Brazoria-Physostegia-Macbridea* clade.

Leaf anatomy has provided strong support for a *Physostegia-Brazoria* clade and weaker support for a clade composed of these plus *Macbridea*. The question still remains whether there is any anatomical evidence to link these three genera to the rest of subtribe Melittidinae or to other genera within tribe Lamieae. Two ingroup genera, *Galeobdolon* and *Synandra*, are suggested as possible relatives of the *Physostegia-Brazoria-Macbridea* clade on the basis of shared nonuniversal derived states; an expanded survey of the Lamieae may reveal other relatives. Diallelocytic-2 stomata are shared by *Physostegia*, *Brazoria*, *Macbridea*, and *Galeobdolon*. Subsessile glands with partial radial walls (types 7 and 10) occur in *Physostegia*, *Brazoria*, *Macbridea*, and *Synandra*.

Leaf anatomy has provided no evidence that subtribe Melittidinae is monophyletic. The four North American genera may form a clade, but *Galeobdolon* (which has never been treated as belonging to the subtribe) is no less strongly implicated than *Synandra* as the sister group of the *Physostegia-Brazoria-Macbridea* clade. No anatomical characters suggest a relationship between *Chelonopsis* or *Melittis* and the rest of the Melittidinae. Since leaf anatomy, floral morphology, and karyology (Cantino, 1985a) do not provide any convincing evidence that subtribe Melittidinae is monophyletic, nor does any other character we are aware of, its abandonment should be seriously considered.

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APPENDIX 1. Abbreviated collection data for
voucher specimens.*

- Ajuga reptans* L. Ohio, Athens Co., Athens, *Cantino* 1217.
Blephilia hirsuta (Pursh) Benth. Ohio, Vinton Co., Lake Alma State Park, *Cantino & Abu-Asab* 1249.
Brazoria arenaria Lundell. Texas: Aransas Co., Aransas National Wildlife Refuge, *Kessler* 5773; Refugio Co., *Kessler* 5771.
Brazoria pulcherrima Lundell. Texas, Leon Co., *Kessler* 5862, 5865.
Brazoria scutellarioides Engelm. & Gray. Texas, Travis Co., *Sanders* 76168 (TEX), 76179 (TEX).
Brazoria truncata (Benth.) Engelm. & Gray. Texas, Live Oak Co., 2 km SW of Whitsett, *Sanders* 76122 (TEX).
Chelonopsis forrestii Anthony. China, Szechwan Prov., *Rock* 5515 (A).
Chelonopsis moschata Miq. Japan, Prov. Iwashiro, Pref. Fukushima, *Furuse s.n.*, 7-IX-1957 (A).
Galeobdolon luteum Hudson. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino* 1271.
Lamium purpureum L. Ohio, Athens Co., Athens, *Cantino* 1214.
Leonurus cardiaca L. Michigan, Ingham Co., East Lansing, *Cantino* 1224.
Macbridea alba Chapman. Florida, Bay Co., E of Callaway, *Godfrey* 79884.
Macbridea caroliniana (Walter) Blake. North Carolina, Pender Co., near Long Creek, *Cantino* 1204.
Marrubium vulgare L. Ohio, Athens Co., Athens, in garden, *Cantino* 1242.
Melittis melissophyllum L. Czechoslovakia, Brünn [Brno], *Piskoi* 667 (GH); France, between Cependu and Moux, *Neyraut s.n.*, 12-VI-1888 (GH).
Monarda fistulosa L. Ohio, Vinton Co., Vinton Twp., *Cantino & Abu-Asab* 1251.
Physostegia angustifolia Fern. Louisiana, St. Tammany Parish, 10 mi SW of Covington, *Cantino* 1058.
Physostegia digitalis Small. Louisiana, Rapides Parish, 3 mi N of Elizabeth, *Cantino* 1070 (GH).
Physostegia godfreyi Cantino. Florida, Gulf Co., 12 mi S of Wewahitchka, *Cantino* 1054.
Physostegia leptophylla Small. North Carolina, Hertford Co., 4 mi W of Winton, *Cantino* 971 (GH).
Physostegia longisepala Cantino. Louisiana, Lafayette Parish, garden plant transplanted from vicinity of Mauriceville, Orange Co., Texas, *Vincent* 4291.
Physostegia purpurea (Walter) Blake. North Carolina, Harnett Co., 3 mi SE of Bunnlevel, *Cantino* 939.
Physostegia virginiana (L.) Benth. subsp. *praemorsa* (Shinners) Cantino. North Carolina: Transylvania Co., 4 mi SW of Lake Toxaway, *Cantino* 946; Montgomery Co., 0.5 mi N of Blaine, *Cantino* 943 (GH).
Physostegia virginiana (L.) Benth. subsp. *virginiana*. Ohio, Athens Co., York Twp., *Cantino* 1260.
Pogostemon cablin Benth. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino* 1262.
Prostanthera rotundifolia R. Br. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino* 1261.
Scutellaria elliptica Muhlenb. Ohio, Jackson Co., Lake Alma State Park, *Cantino & Abu-Asab* 1222.

*Vouchers at BHO unless otherwise indicated. Herbarium abbreviations follow Holmgren *et al.* (1981).

- Scutellaria incana* Biehler. Ohio: Athens Co., Athens, *Cantino & Abu-Asab* 1236; Hocking Co., Ward Twp., *Cantino & Abu-Asab* 1247.
- Scutellaria integrifolia* L. Ohio, Vinton Co., Lake Alma State Park, *Cantino* 1227.
- Scutellaria lateriflora* L. Ohio. Vinton Co.: Lake Alma State Park, *Cantino & Abu-Asab* 1248; Lake Hope State Park, *Cantino & Abu-Asab* 1257.
- Scutellaria nervosa* Pursh. Ohio: Athens Co., Athens, *Cantino* 1231; Perry Co., Monroe Twp., *J. Young s.n.* (no voucher).
- Scutellaria ovata* Hill. Ohio, Athens Co., Athens Twp., *Cantino* 1232.
- Scutellaria serrata* Andrz. Ohio. Vinton Co.: Brown Twp., *Cantino & Abu-Asab* 1219; Lake Alma State Park, *Cantino & Abu-Asab* 1221.
- Stachys riddellii* House. Ohio, Vinton Co., Lake Alma State Park, *Cantino* 1229, 1230.
- Stachys tenuifolia* Willd. Ohio. Athens Co.: Athens, *Cantino* 1235; Waterloo Twp., *Cantino & Abu-Asab* 1253. Vinton Co., Lake Hope State Park, *Cantino & Abu-Asab* 1256.
- Synandra hispidula* (Michaux) Baillon. Ohio, Morgan Co., Union Twp., *Cantino* 1151.
- Teucrium canadense* L. Ohio, Athens Co., Dover Twp., *Cantino & Abu-Asab* 1243, 1244.
- Teucrium chamaedrys* L. Ohio, Athens Co., Athens, in garden, *Cantino* 1240.
- Trichostema dichotomum* L. Ohio, Perry Co., Monroe Twp., *J. Young s.n.*, 24-VIII-1983.
- Trichostema lanceolatum* Benth. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino* 1259.

APPENDIX 2. Classification of sessile glandular trichomes in the Labiatae.*

- Type 1. Head composed of one cell.
- Type 2. Head composed of two cells (FIGURE 5f1).
- Type 3. Head composed of three cells.
- 3a. Head divided by two transverse walls (FIGURE 5a6).
- 3b. Head divided by three radial walls (FIGURE 5f2, g1).
- Type 4. Head composed of four cells (FIGURE 5a1, b1, d1, e1, f3, g2, h1).
- Type 5. Head of more than four cells, usually divided by four primary radial walls that are more or less perpendicular to each other; tertiary and tangential walls absent; no more than one secondary radial wall arising on a given side of any primary radial wall (FIGURE 5a2-5, b2, c1, c2, d2, d3, e2, g3, h2).
- Type 6. As in Type 5, but with tangential walls present (FIGURE 5d4).
- Type 7. As in Type 6, but with partial radial walls present (FIGURE 5e3).
- Type 8. Head of more than four cells; tertiary radial walls present and/or more than one secondary radial wall arising on the same side of at least one primary radial wall; tangential walls absent (FIGURE 5a7).
- Type 9. As in Type 8, but with tangential walls present; partial radial walls absent (FIGURE 5a8, c3).
- Type 10. As in Type 9, but with partial radial walls present (FIGURE 5a9, b3).

*Cell-wall configurations are defined in the text and illustrated in FIGURE 4.

**APPENDIX 3. Leaf histological characters of
possible taxonomic value.**

1. Mesophyll differentiation: a, undifferentiated; b, bifacial; c, isobilateral.
2. Compactness of palisade cells: a, compact; b, loose.
3. Idioblasts in mesophyll: a, absent; b, saclike; c, resembling internal glandular trichomes.
4. Fibers associated with midrib: a, absent; b, present only on adaxial side of midrib; c, present only on abaxial side of midrib; d, present on both sides of midrib.
5. Collenchyma associated with midrib: a, absent; b, present only on abaxial side of midrib; c, present on both sides of midrib.
6. Bundle-sheath extensions: a, absent; b, present only on abaxial side of bundle; c, present on both sides of bundle.
7. Prominence of keels associated with vascular bundles as viewed in transverse section of lamina: a, keels absent; b, secondary veins lacking keels, midrib keel protruding slightly; c, secondary veins lacking keels, midrib keel protruding greatly; d, secondary veins keeled, midrib keel protruding slightly; e, secondary veins keeled, midrib keel protruding greatly.

Erratum—The *Pogostemon* used in this study was *P. heyneanus* Benthams, not *P. cablin* Benthams.